Sago Pondweed (*Potamogeton pectinatus* L.): A Literature Review

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By Harold A. Kantrud

Contents

Frontispiece. Calm areas in this lake are beds of sago pondweed (*Potamogeton pectinatus* L.) whose densities can reach 840 individual plants per square meter. Sago normally occurs in bodies of permanent water, as in this prairie lake in North Dakota.

Sago Pondweed (*Potamogeton pectinatus* L.): A Literature Review

by

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ABSTRACT.—Sago pondweed (*Potamogeton pectinatus* L.) is a submersed macrophyte of nearly cosmopolitan distribution. The plant is of worldwide importance as a waterfowl food but also can be a nuisance in irrigation canals and recreational areas. The plant reproduces by many different means, depending on habitat and environmental stress. Several genetic ecotypes have evolved. Most important as waterfowl food are the turions (tubers), vegetative propagules rich in carbohydrates that are mostly buried in bottom sediments. In temperate wetlands, most turions sprout in spring, making sago behave as an annual. Drupelets (seeds) are the sexual propagules of sago and provide a mechanism for sago to survive periods of drought and excessive water salinity. Drupelets can be washed ashore or carried by birds for long distances. Sago decomposes rapidly at senescence, annually in temperate wetlands.

Sago is mostly found in semipermanently or permanently flooded mixosaline lacustrine, palustrine, and riverine wetlands <2.5 m deep, where fetches are not large or currents are <1 m/s. Sago seems to prefer stable water levels but can tolerate significant water level fluctuations. Among the *Potamogetons*, only sago tolerates high salinity, pH, and alkalinity, but it fares poorly among specialist taxa in acidic or nutrient-poor waters. Sago is highly tolerant of eutrophic waters, and it can be the only species of submersed macrophyte present in heavily polluted sites. Sago grows in nearly all bottom substrates. Turbidity is the factor that most frequently limits sago growth.

Sago often occurs in monotypic stands but can grow with many other submersed and emergent macrophytes. Dominance by sago in certain wetlands sometimes alternates with dominance by other submersed macrophytes when salinities or other environmental factors change. Sago also can be associated with a large variety of unattached filamentous, planktonic, or epiphytic algae. Increased turbidity caused by planktonic algae often is responsible for lowered sago production. Less common biotic limiting factors are organic pollutants and consumption and uprooting by waterfowl and fish.

Sago provides food or shelter for amphibians, reptiles, fish, and mammals. The greatest value of sago in North America is as food for migrant and staging waterfowl, primarily diving ducks and swans. Sago beds also provide habitat for a large complex of invertebrates (an important food source for young waterfowl), but direct consumption of living sago by invertebrates is negligible.

Sago has been propagated for many years—indoors, as an experimental organism for work in plant physiology or herbicide testing, and outdoors, for purposes of attracting waterfowl. Much work has also been done developing methods to control excessive sago growth in fishponds and irrigation canals.

Future research should concentrate on (1) determining, in a variety of wetland types, the causes of light-limiting turbidity that often suppresses sago growth, (2) understanding the ways in which human activities on and near wetlands affect sago production, and

(3) developing reliable and predictable techniques to stimulate sago production for waterfowl by using water level manipulations and other means, in a variety of environmental settings.

"...so protean are their (*Potamogeton*) forms, so
eccentric their action, constantly changing under
changed conditions of season and water, that I put
forth this treatise with great diffidence, and feel that
the subject is very far from being exhausted."

Thomas Morong, 1893

Throughout the world, communities of submersed angiosperms are important feeding and rearing habitats for waterfowl, fish, and many other organisms. Some of the most important of these communities to waterfowl are dominated by sago pondweed (*Potamogeton pectinatus* L.), which is unique among *Potamogeton* taxa in its nearly worldwide distribution and often great abundance in monotypic stands. The importance of sago to staging and migrant waterfowl is so great that, at least in North America, continental migration pathways of some species can be determined by the location of large water bodies dominated by the plant. Unfortunately, the abundance of sago (and other important waterfowl food plants) has declined drastically in many wetlands that have a history of substantial use by staging and migrant waterfowl. Therefore, efforts are currently under way in several areas of the United States to restore sago and other submersed macrophytes to their former abundance. The success of these endeavors will require a thorough knowledge of the life histories and environmental requirements of the plants involved.

There are several brief life histories of sago (Moore 1915; Yeo 1965; Stevenson and Confer 1978; Wallentinus 1979) and many reports on the effects of several environmental variables on the distribution and abundance of the plant in many parts of the world (e.g., Craner 1964; Aleem and Samaan 1969a,b; Kollman and Wali 1976; Anderson 1978; Howard-Williams and Liptrot 1980; Verhoeven 1980a,b; Van Vierssen and Verhoeven 1983; Van Wijk 1988). Sago is easily cultured in pure liquid media in the laboratory but is also a nuisance plant that clogs irrigation facilities and interferes with fishing and recreational boating. These attributes have resulted in much information on sago physiology and control methodology that can be useful to waterfowl managers. In addition, there are numerous references to use of sago by waterfowl and to

methods whereby sago production can be increased to attract greater numbers of waterfowl.

There have been no recent attempts to assemble and synthesize the available information on sago, despite its nearly worldwide ecological importance. I have tried to assemble such information in this report so that sago can be properly protected and managed. Some material is included that is possibly of interest only to specialists. This report is largely based on material in English or with English summaries, but much foreign material, often not seen by me but cited by other authors, is included. Not included are many references to the simple occurrence of sago in various wetlands worldwide, early taxonomic studies, mostly foreign, of sago, and reports of tests of potential chemical control agents.

Classification and Distribution

The valid scientific name for sago is *Potamogeton pectinatus*, assigned by Linnaeus in his *Species Plantarum* of 1753. The name *Potamogeton* is derived from the Greek for "river neighbor," and the specific epithet *pectinatus* ("comb-like") derives from the closely set insertion of the plant's leaves. The synonyms *P. interruptus* Kit., *P. latifolius* J. W. Robbins, *P. flabellatus* Bab., and *P. columbianus* Suksdorf have been used in North American botanical texts. Many other synonyms have been used in Europe. Two modern treatments, Kartesz and Kartesz (1980) and United States Department of Agriculture (1982), recognize 40 and 35 North American species of *Potamogeton*, respectively, and place the genus in the family Potamogetonaceae. Earlier, the genus had variously been placed in the families Zosteraceae and Najadaceae (Fernald 1950). There are about 100 species of *Potamogeton* worldwide (Kadono 1982). Sago flowers and leaves are simple and anatomically reduced, compared to those

of other family members (Sculthorpe 1967). Sago was one of the first *Potamogeton*s to be described. An illustration of "fennel-leaved water milfoile" is easily recognized as sago in the ancient herbal of John Gerarde (Johnson 1633; Moore 1915). An excellent history of the genus is available (Moore 1915).

Colloquial names for sago in the United States include duck grass, duck moss, eelgrass, fennel pondweed, foxtail, Indian grass, old-fashioned bay grass, pondgrass, potato moss, and wild celery (McAtee 1939). In Europe, sago has been called poker and pochard grass (McAtee 1917) and, in Australia, string weed (Fletcher et al. 1985).

In North America, sago is placed with *P. filiformis* and *P. vaginatus* in the subgenus *Coleogeton*, in which all leaves are linear or setaceous, nonfloating, and divided their full length by crosspartitions (Fernald 1950). Harrison (1949) claims members of this subgenus are, unlike others, waterpollinated. The three coleogetonous species have also been shown to form a distinct subgroup based on the chemistry of the waters they inhabit (Pip 1987). In the field, sago can be differentiated from the two other coleogetonous species by the presence of usually sharp-tipped or gradually pointed leaves and leaf sheaths that are rather narrow but free at the tips.

Sago has an average of 2n = 78 (70–87) chromosomes (Kalkman and Van Wijk 1984). Analyses of isoenzymes indicated that the species is genetically very heterogeneous (Hettiarachchi and Triest 1986; Van Wijk et al. 1988). Sago hybridizes with *Potamogeton filiformis* (*P*. × *suecicus* Richt.) and *P. vaginatus* (Hagstrom 1916; Dandy and Taylor 1946; Harrison 1949). Meriaux (1978) and Van Wijk (1988) reviewed the work of many European taxonomists who named many varieties or "proles" of sago (*dichotomus* Wallr., *drupaceus* Koch, *flabellatus* Crep., *interceptus* Asch., *protensus* Wallr., *setaceus* Mey., *scoparius* Wallr., *vulgaris* Cham. and Schl., and *zosteraceus* Fries). Both questioned whether these are simple morphs or truly have value as indicators of specific biotopes or habitat types. Luther (1951, cited in Van Wijk 1983) also concluded that the different types of sago were habitat modifications. The varieties *interruptus* Asch., *pectinatus*, and *scoparius* have been maintained in a recent European flora, although their taxonomic validity is said to be unclear (Casper and Krausch 1980, cited in Van Wijk 1988). Van Wijk (1983) found different morphological and ecological characteristics of annual and perennial *P. pectinatus* in the field and in cultured plants and recommended that the existence of these ecotypes be considered when studying the taxon. Wiegleb (1978) associated the variety *scoparius* with HCO_3-poor waters and the variety *interruptus* with sites polluted with sewage. Recent work has shown that genetic differentiation does occur in sago and must be considered along with morphological characters if the taxonomy of the species is to be clarified (Van Wijk et al. 1988).

Autecological Classification

Sago is one of only three or four North American species of *Potamogeton* that bear starchy underground perennating organs called turions or tubers, although a few other species have tuberous rootstalks. Sago is generally classified as a ruderal (capable of occupying mechanically disturbed areas), has multiple regenerative strategies, and is a stress-tolerant, competitive plant that, depending on exposure to wave action, can alter its allocation of resources to different reproductive organs (Grime 1979; Kautsky 1987). In growth form, sago is considered a parvopotamid—that is, a higher aquatic plant rooted in sediment, perennially submersed except for inflorescences, and possessing long stems and small, mostly undivided, leaves (Hutchinson 1975). Luxuriant parvopotamid growth results in dense leaves, branches, and inflorescences in the upper part of the water column, with much thinner vegetation of stems and widely spaced leaves below; vegetation density of the upper part increases as water levels drop (Verhoeven 1980a).

Meriaux (1978) reviewed the work of devotees of the Zurich-Montpellier school of phytosociology (Braun-Blanquet 1932) who placed sago in various orders, alliances, and associations with other species in this elaborate phytosociological classification system. Sago was also recognized as a character or dominant species in several European and Asian associations by Hejny and Husak (1978). Sago is the most prominent plant in the *Potamogeton* facies of several estuarine plant communities in Europe (Kornas et al. 1960) and a faithful taxon in the class Potamea (den Hartog and Segal 1964) in some wetlands in India (Zutshi 1975). Sago also is a member of several *Chara*-, *Ruppia*-, and *Zannichellia*-dominated communities in the Baltic, Mediterranean, and Eurosiberian regions (Lindner 1978; Verhoeven 1980a; Van Vierssen 1982a).

Sago can be considered a pioneering species, because it quickly inhabits newly flooded areas (Nelson 1954) and invades shallow waters with relatively strong wave action (Ozimek and Kowalczewski 1984) or those that are polluted (Haslam 1978). Sago is one of the first species to colonize areas reclaimed from the sea (Wolseley 1986). den Hartog (1963) and Van Vierssen (1982a) considered sago a survivor species that often showed mass development in areas where the environment became temporarily unsuitable for other species. Davis and Brinson (1980) placed sago in a group of plants tolerant of, and able to maintain dominance in, altered ecosystems.

Sago is found in submerged, floating-leaved, and emergent communities. Best plant development occurs in submerged communities, and the poorest in emergent communities where sago plants tend to be short in stature (Van der Valk and Bliss 1971). In general, most other growth forms of hydrophytes, except similar types such as charids, valisnerids, and ceratophyllids, negatively influence the environment for parvopotamids, usually because of competition for light (Hogeweg and Brenkert 1969).

Most submersed macrophytes are sensitive to frost damage (Lohammar 1938). This, combined with the rapid decomposition of plants in water, causes sago to usually behave as an annual in shallow waters in temperate climates, with buried turions the only vegetative structure to survive winter (Lapirov and Petukhova 1985). However, green sago shoots can be collected under winter ice, presumably in deeper waters (Hammer and Heseltine 1988). Turions are perennial diaspores formed underwater and take several weeks or months to develop. The fruit-like seed (drupelets) can require a stratification period to germinate well in areas of fairly mild climate. These findings, plus the observation that sago could not compete well in shallow water against species that produce seeds (annual diaspores) more quickly, led Van Vierssen and Verhoeven (1983) to consider sago a species rather intolerant of habitat desiccation.

In mild climates sago can be evergreen (Spence et al. 1979b). Rarely, some deepwater forms of sago grow perennially from submersed rootstalks and can also have green shoots that survive winter (Moore 1915). Sago can behave as an annual by dying under conditions of high salinity and regenerating from drupelets when salinity decreases (Congdon and McComb 1981). When sago is compared to *Potamo-*geton nodosus*, a species that forms winter buds rather than turions, both species invest about the same amount of photosynthate in perennating structures, but sago produces about twice as many propagules (Spencer and Anderson 1987).

The functional aspects of sago's ability to thrive and survive in a wide variety of environments have been addressed in detail by Van Wijk (1988) and will be discussed in later chapters. Van Wijk (1988) points out the confusion that has resulted from use of the terms annual and perennial to categorize plant types as well as life-cycle types, and argues that they should only be used to indicate life cycles of populations without implying a classification of plant species. Under this system, sago could theoretically be said to have an annual life cycle with either (1) generative reproduction by seeds or vegetative reproduction by turions or thickened rhizomes or (2) a perennial life cycle with vegetative reproduction by whole plants or shoots. Not all of these strategies have been observed in nature.

In Europe, the *Potamogeton pectinatus* association is often linked to brackish water (den Hartog 1963) and inland marshes and depressions affected by mineral pollution (Meriaux 1978). den Hartog (1981) placed sago with a small group of plants that share many properties with marine angiosperms but cannot compete well with them except under special circumstances. He termed sago a member of the eurysaline group of plants in that they are able to tolerate waters from fresh to hyperhaline that vary greatly in chemical composition. These plants are also able to withstand rapid and considerable fluctuations in salt content of the waters they inhabit. Iversen (1929) included sago in a group of species restricted to alkaline waters. Lohammar (1938) found sago in lake waters characterized by both high pH and calcium content. Further analysis of Lohammar's data by Hutchinson (1975) showed sago to be a eurytopic species able to tolerate a wide range of nutrient (nitrogen, phosphorus) concentrations. Moyle (1945) placed sago in an assemblage of hard water species able to withstand waters high in sulfate ion. Other classifications based on water chemistry have been proposed by Spence (1967) and Seddon (1972).

Distribution

Unlike most of the *Potamogeton*s, which are interior and northern in global distribution, sago is

nearly cosmopolitan (St. John 1916). The plant occurs circumboreally to about 70° N (Hulten 1968) and can also be found in South Africa, South America, South Eurasia, and New Zealand. The species occurs from sea level to nearly 4,900 m above sea level in high mountains of Venezuela and Tibet (Ascherson and Graebener 1907, cited in Yeo 1965). Pip (1987) recorded 19 species of *Potamogeton* at 430 wetland sites distributed throughout a large area of central North America and found sago second only to *P. richardsonii* in frequency of occurrence.

Development and Reproduction

Except where specific references are given, the information in this section was excerpted from the sources listed in Table 1 and standard botanical texts.

Roots

Sago, like most submersed vascular plants, is ecologically adapted to grow with its roots in sediments that have low oxygen levels. The vascular system of sago is poorly developed (Arber 1920; Sculthorpe 1967), and roots are proportionally small. These features are indicative of hydrophytes that absorb more nutrients from the water column than from the bottom substrate (Hutchinson 1975). In sago, bundles of four or more roots form on nodes along the rhizome. Main roots are colored white to light tan, about 0.2 mm wide, and 2–4 cm long (H. A. Kantrud, personal observation). Sago roots penetrate the bottom to at least 0.5 m in sands, but are found at much shallower depths in finer sediments. Sago

Table 1. *References and subject material about the development and reproduction of sago pondweed* (Potamogeton pectinatus *L.).*

Reference	Subjects covered
Moore 1915	Early *Potamogeton* literature and field observations
Muenscher 1936a,b	Germination tests
Sharp 1939	Propagation trials
Harrison 1949	Aspects of life history
Teeter 1963, 1965	Effects of NaCl on growth and reproduction
Craner 1964	Production and use by waterfowl
Yeo 1965	Drupelet germination and propagation by turions
Hodgson 1966	Rhizome and shoot development
Ogg et al. 1969	Turion production
Paullin 1973	Ecology
Anderson 1976; Anderson and Low 1976	Production and use by waterfowl
Verhoeven 1980a,b	Life history and habitat preferences (Europe)
Howard-Williams 1978, 1981; Howard-Williams et al. 1978; Howard-Williams and Davies 1979; Howard-Williams and Liptrot 1980; Howard-Williams and Allanson 1981	Life history, habitat preferences, and nutrient cycling (Africa)
Wallentinus 1979	Production rate
Purohit 1981	Phytosociology, growth behavior, and germination
Van Vierssen and Verhoeven 1983	Reproductive behavior
Van Wijk 1983	Germination
Ozimek et al. 1986	Biomass allocation and growth rates
Madsen 1986	Temperature effects and leaf morphology
Spencer 1986a,b, 1987	Morphology, pigments, turion demography, and temperature and light effects
Spencer and Anderson 1987	Effects of photoperiod on growth
Van Wijk 1988, 1989; Van Wijk et al. 1988	Reproduction, biomass, and interspecific variation

branches will become rooted in bottom sediments (McAtee 1939).

Rhizomes

There is general disagreement in botanical texts as to the precise definition of runners, rootstocks, rhizomes, and stolons, especially as to whether these structures are modified stems or branches, whether they occur above ground, below ground, or both, and whether they root at the tips, nodes, or both. I have elected to use the term rhizomes for the white, often extensively matted, structures by which sago plants spread extensively across bottom substrates. Rhizomes are 1.5–5.0 mm wide. Rhizomes first emerge from the third or fourth node of the main stem as it develops from a sprouting turion. Later rhizomes also develop from the main stem. Rhizomes emerge from the bottom substrate, bear a leafy shoot on alternate nodes, and then arch downward to reenter the substrate. Roots and turion-bearing branches grow downward from the leafy shoot as it comes in contact with the substrate. The alternate node is bare. A rhizome can have seven shoots at 4 weeks. Healthy 13-week-old plants can bear 22 rhizome shoots.

Vegetation

In temperate climates, sago is one of the first submersed plants to begin spring growth. Elongation begins in various hibernating organs when water temperatures reach about 10°C—from late March to late June in the Northern Hemisphere. Plants reach the water surface in May to mid-July, and, about 2 weeks later, healthy stands can cover much of the water surface. Plants can reach the water surface more rapidly under low light conditions common in eutrophic or brackish waters.

Vegetative branching is sympodial. A main stem is first to reach the surface; several rhizome-derived stems reach the surface several weeks later. Stem length is determined by water depth and movement.

Branching is dense (Figure), but some growth forms lack the densely branched canopy near the water surface. Biomass of these growth forms can be greatly reduced (Kautsky 1987).

Leaves may grow up to 35 cm long, 0.25–2.5 mm wide, and 0.18–1.07 mm thick. Leaf tips can be sharply pointed, gradually tapered, or variable on a single older plant (Mason 1969), and other leaf characteristics can also vary greatly on a single plant. Leaves are covered with a waterproof cuticle 0.1 μm thick, greater than found in many other submersed macrophytes (Sharpe and Denny 1976). It has been hypothesized that the fine linear form of leaves, such as found on sago and other submersed species that live in waters with fluctuating salinity, is an adaptation whereby the area of epidermal cells assumed to provide two-way transport of electrolytes is great compared to leaf volume, thus aiding osmoregulation (Verhoeven 1979).

The 3–7 veined leaves have ligules 4–12 mm long and tightly clasping sheaths 8–30 mm long. The number of veins and leaf width have been observed to increase in plants cultured in nutrient-rich solutions.

Growth form of sago varies considerably and may depend on a variety of factors, including shoot density, depth, light climate, bottom substrate, wave action, and waterfowl grazing, rather than genetic differences among populations (Luther 1951, cited in Van Wijk 1988). This is not to say that great genetic variability does not exist in sago populations exhibiting differences in growth form. Leaves of the early growth of sago are much longer and thicker and branches are much less numerous (var. *zosteraceus*) than on the narrow-leaved, profusely branched plants (var. *scoparius*) that form after plants reach the water surface (Howard-Williams 1978). Nearly whole plants of the large, early growth form of sago can wash ashore from deeper waters after being loosened by the feeding activities of spring migrant waterfowl, before any plants can be found in shallower nearshore areas (H. A. Kantrud, personal observation). A gigantic form up to 5.5 m long with extremely long leaves grew in Lake Cayuga, New York (Dudley 1886). Sago vegetation becomes senescent from late August to October in north temperate regions, and most decomposes or washes ashore by the time wetlands freeze. During this period, huge amounts of green sago vegetation and rhizome fragments can wash ashore as a result of disturbance from migrant waterfowl feeding.

Flowers

Flowering, usually considered light-initiated, begins shortly after maximum biomass is attained. Flowering occurs mostly during mid-May to mid-July in the Northern Hemisphere, but in mild climates the flowering phase can extend for up to 5 months (Gupta 1968; Ramirez and San Martin 1984). The dull pink flowers are monoecious, perfect,
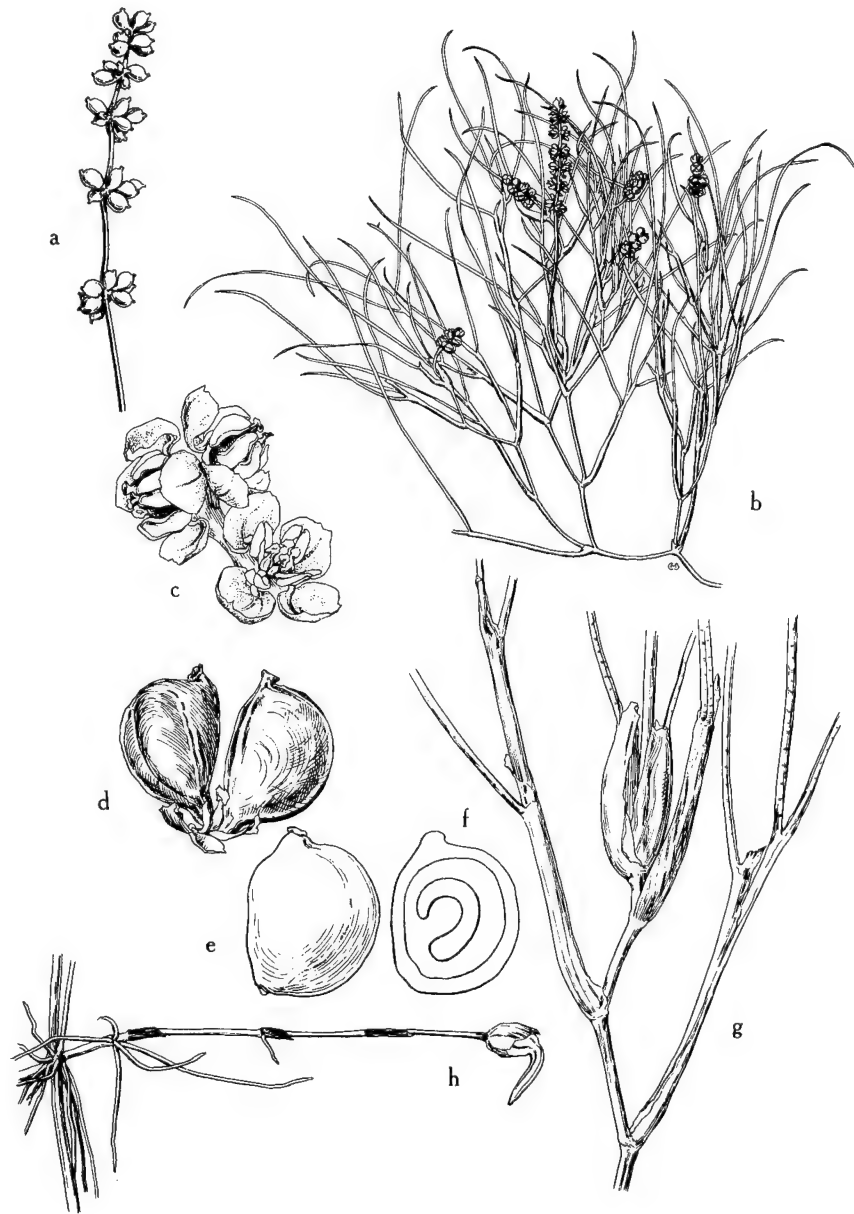
Figure. *Potamogeton pectinatus. a.* Spike with whorls of mature drupelets, × 1.2; *b.* habit, showing rhizomes bearing dense branches with linear leaves, × 0.67; *c.* upper flowers of spike, × 4; *d.* and *e.* drupelets showing short beak: *d,* = 5.5, *e,* × 5; *f.* longitudinal section of drupelet showing outer coat and crescent-shaped embryo, × 5; *g.* stipules sheathing stems, × 3; *h.* rhizome with roots and distal turion, × 1.2. (From Mason 1969; reproduced with permission of University of California Press, Berkeley.)

and borne on a peduncle up to 30 cm long that arises from the tip of a leafy shoot. Floral branching is sympodial. Each flower has four sepal-like connectives, four stamens with large two-locular anthers, and four pistils with one-carpeled ovaries. The flowers are 4 mm wide; 10–15 are crowded in the spike at emergence but later separate into two to six unequally grouped whorls as the spike elongates up to 5 cm and is erected above the water surface (Mason 1969). Pollination is mostly by pollen not derived from the parent plant. Buoyant, translucent pollen is transported along the water surface by air currents. Each anther has 2,500–7,500 large (33–40 μm) pollen grains; these are much larger than in most North American species of *Potamogeton* (Philbrick and Anderson 1987). By mid-June to mid-August, fertilization is complete and drupelet growth begins.

Sexual Reproduction

Sago plants derived from drupelets are uncommon in many permanent wetlands and may mostly occur in semipermanent wetlands as an adaptation to long-term desiccation or drastic changes in salinity. Van Wijk (1983, 1988) seldom observed germinated drupelets or seedling sago plants in nature and concluded that the most important function of these propagules is as a dispersal mechanism. He cited a study by Guppy (1897) that showed that drupelet germination can be enhanced by passage through the gut of a duck. Ridley (1930) also stated that sago drupelets are capable of surviving the digestive systems of birds. Mean retention time of viable sago drupelets in mallard ducks is 44 h; this allows long range dispersal (DeVlaming and Proctor 1968).

Fruit formation in sago begins about 3 weeks after flowering. Fruits of sago are called drupelets, or, by some authorities, achenes. These are small fruits with a pulpy or leathery cover over a stony-walled seed. Usually about two of the four ovaries on each flower develop into drupelets. Drupelets are 3.0–4.0 mm long, 2.5 mm wide, and tipped with a vestigial style base in the form of a short beak (Figure). Each drupelet consists of a whitish crescent-shaped cotyledon and embryo covered with a hard wall and a fleshy greenish coat on the outside. The coat turns reddish brown at maturity. A hinged opening that is unridged and obtusely apexed lies distally to the embryo and provides an exit for the cotyledon upon drupelet germination; this characteristic and the thick, large-celled wall differen-tiate sago drupelets from those of all others in the genus (Martin 1951). About 7 to 20 drupelets mature on a short spike.

In north temperate climates, the starchy drupelets of sago are usually mature by late July to late September. In mild climates, the fruiting phase can extend for 2 months (Ramirez and San Martin 1984). Shortly after maturity the drupelets fall to the bottom or float temporarily and wash ashore in windrows. Seed bank studies show that on some large wetlands nearly all sago drupelets are recovered close to shore (Pederson and Van der Valk 1984). Drupelet germination occurs from late March to early summer in north temperate climates. Drupelets exposed for over a year on dry shorelines will germinate in as few as 4 days if wetted.

Haag (1983) studied sago distribution and drupelet germination from sediment cores taken from a permanent Canadian lake and outlined many of the factors that limit the success of sexual reproduction. In waters <2 m deep, physical damage, caused by semifloating masses of detached plant material and burial by litter, resulted in high mortality and prevented many seedlings from reaching maturity. Seedlings in deeper sites often lacked proper light, growing time, and nutrients, and the plants assumed a spindly growth form that rarely flowered. Thus low seedling survival in deep and shallow water becomes combined with low drupelet production to restrict sexual reproduction. Haag (1983) also thought that sago production from drupelets could be limited by relatively short dispersal distances and burial in dark sediments of low reduction-oxidation (redox) potential.

Asexual Reproduction

The asexual or vegetative propagules of the *Potamogeton*s are termed winter buds, winter corms, tubers, and turions in standard American botanical texts, and called bulbs by at least one African authority (Vermaak et al. 1983). Muenscher (1944) termed the axillary winter buds of the genus turions, but labeled diagrams of the subterranean propagules of sago as tubers. There seems to be some general agreement among taxonomists that bulbs and corms are thickened stems that are usually oriented vertically, while tubers are thickened—often fleshy rather than solid—portions of stems, rhizomes, or branches that often have numerous buds or eyes, as in the potato. I have elected to use the term turions

for the solid, scaly, and carbohydrate-rich vegetative propagules of sago.

Potamogeton turions can be either dormant or nondormant. The latter does not require preconditioning before germination. Dormant propagules are called hibernaculae (Sculthorpe 1967). These require preconditioning and a specific environment, usually controlled by light and temperature, to germinate. It is unknown how dormancy is controlled and whether sago produces both turion types in tropical regions (Madsen 1986).

Production of underground turions begins when the main stem of an older plant sends out a horizontal rhizome near the surface of the bottom substrate. The rhizome then penetrates the substrate and forms branches at every other node. Specialized tissue at the tips of the branches forms the turions. In favorable habitat subterranean turions can far outnumber mature drupelets and can be the only reproductive structure on some plants. Turions can also form in leaf axils at the tips of leafy shoots above the bottom surface. Production of this type of turion likely indicates sago populations geared to the relatively short growing season of plants with an annual life cycle. Some authorities claim turions are formed during most of the growing season, whereas others state turion formation begins after peak plant biomass is attained.

Turions (Figure) consist of two swollen internodes. The thickened starchy portion can reach 1.5 cm long. Fresh weight of underground turions is 0.9–1,001 mg. Dry weight is about 30% of fresh weight. Young turions are noticeably smaller than the old. Glasshouse experiments indicate that heavier turions produce larger plants that reach the water surface earlier and produce more shoots (Spencer 1986b). Subterranean turions occur singly or in simple or branched chains of up to five. Chains are up to 8 cm long. Axillary turions are smaller and occur singly or in chains of two. These can serve as a dispersal mechanism (Kautsky 1987). The occurrence of multiple turions may be caused by genetic differences in populations.

Turions can be found to 47 cm below the surface of the bottom substrate. Studies are inconclusive as to whether turion number varies with depth below bottom substrate, at least for depths >7.5 cm. Mean turion weight may be greater in sago populations exhibiting perennial, versus annual, life cycles. Larger turions tend to occur deeper in the subtrate, at least in irrigation canals. Some studies indicate

that this occurs because smaller axillary turions separate from parent plants and drop to the bottom as the fall dormant period begins. Others attribute the phenomenon to the feeding activities of waterfowl, or to the possibility that it represents an important adaptation that enables sago to survive desiccation. Small (<10 mg fresh weight) turions planted shallowly (<10 cm) produce plants with reduced growth rates and number of ramets per plant compared to those grown from larger turions. Turions of all weight classes planted at 20 cm produce plants with reduced growth rates. Smaller turions and turions planted deeper show reduced emergence. Thus turion size and depth distribution in sediments may be important environmental factors that regulate sago growth.

Turion development peaks in late summer or early fall in north temperate regions. Turions in storage can remain viable for several years (F. Nibling, U.S. Bureau of Reclamation, personal communication); they can survive in exposed mud for a year in temperate climates (Van der Valk and Davis 1978). Published studies do not report how long turions remain viable in nature, but data of the U.S. Bureau of Reclamation (Garrison Diversion Unit Refuge Monitoring Annual Reports, Bismarck, North Dakota, 1987, 1988, 1989, unpublished) suggest that turion density accumulates from more than 1 year's growth.

Most sago reproduction in nature is from turions that simultaneously send up shoots and develop extensive subterranean systems of rhizomes that send up additional shoots in great abundance. Production of leafy shoots also occurs through axillary buds, stem or rhizome fragments, and thick woody rootstalks that can be buried more than 15 cm in bottom soils. At the beginning of the growing season in thalassic Swedish waters, nearly 100% of existing sago biomass in exposed sands can be in the form of turions, whereas in sheltered muds, 75% of the biomass can consist of overwintering shoots (Kautsky 1987).

As early as late March in the Northern Hemisphere, overwintering turions begin to develop a long shoot bud that develops leaves at the tip and rhizomes and roots on lower nodes. A dormant bud develops if the main bud is severed. Not all turions germinate each spring, at least in temperate waters (M. G. Anderson, personal communication). Turions have highest germination rates during certain months and germinate regardless of light

climate, even though light may aid germination, especially of the shoot portion. Light intensity seems unimportant.

Maximum germination and growth of turions occurs over a broad temperature range—15–26° C—and germination temperatures as low as 5.5° C have been recorded in the field. Turions from temperate climates require cold preconditioning (stratification) for good germination. Temperatures exceeding 30° C may damage proteins and inhibit germination.

Turions have been experimentally germinated while suspended in the water column at depths of 10 m, but best germination occurred at 1.0 m, where, after 24 days of growth, means of 8.8 leaves per plant and 4.9 roots per plant were recorded; at 10 m (where pressure was in excess of 1 atm.), leaf and root production was 90% lower. Turions can grow normally when suspended at 5 m depth even though Secchi depth is only 82 cm. In the laboratory, turions can be germinated in the dark, which suggests that excess pressure, rather than low light conditions, inhibits sago colonization beyond 5 m depths.

After 30 days of growth, a turion can have developed a main stem bearing 2 rhizomes that have a total of 11 shoots. Laboratory tests show the carbohydrate reserves in turions are exhausted in 3 weeks. Turions can continue growth for several years. Young, small turions germinate within 10 days in culture, but old, large turions can require a resting period of up to 110 days. Surface water or ice cover is not necessary for overwinter turion survival. They are, however, sensitive to desiccation, as up to 60% of turions exposed for 2 weeks to sediment moistures <23% failed to germinate.

Some investigators have found that quiescent stems and bristly apical shoots serve as vegetative propagules in sago, whereas others could not detect the ability of the plant to grow from detached fragments that bore buds or nodes.

Physiology

Sago is well suited to laboratory culture. Its physiology is known partly from studies on the uptake of herbicides tested to reduce sago's presence in irrigation canals.

Welsh and Denny (1979) showed that P moved both from and into sago shoots. Huebert and Gorham (1983) examined the ability of sago roots to mobilize nutrients from a constant small volume of sediment in the absence of one or more of the nutrients from the water column. Roots were capable of mobilizing sufficient N, P, potassium, sulfur, and micronutrients from the sediment to the shoots to meet normal growth requirements. In the absence of K from the water phase, sodium replaced it, although plant vigor suffered. Roots could not mobilize enough magnesium, calcium, or dissolved inorganic carbon from the sediment to the shoots to meet normal growth requirements. They speculated that the exclusion of sago and other species from waters of low alkalinity can be caused by the water-phase inorganic C requirement of these plants. They also suggested that water-phase Ca was necessary to prevent toxicity of other cations when they are present in the water phase (see Water Column Chemistry).

Sago uses HCO_3 during photosynthesis but has a higher affinity for CO_2 (Sand-Jensen 1983). Production may be reduced by the excess energy required to use HCO_3 as a carbon source, but the formation of monotypic stands of sago in saline environments may result from the plant's ability to use HCO_3 and simultaneously withstand osmotic stress (Kollman and Wali 1976). The lower surface of *Potamogeton* leaves is involved in HCO_3 use, and the upper for OH release (Prins et al. 1980).

Total chlorophyll content of sago is 0.81 mg/g fresh weight (Madsen 1986). Chlorophyll a, b, and carotenoid content of sago have also been reported (Spencer 1986a; Azcon-Bieto et al. 1987; Spencer and Anderson 1987; Spencer and Ksander 1987; Penuelas et al. 1988). Pigment concentrations are probably lower in sago stems and leaves than in several other common submersed angiosperms (Azcon-Bieto et al. 1987; Spencer and Anderson 1987; Penuelas et al. 1988). This could be an adaptation to the low levels of light or high concentrations of forms of carbon other than CO_2 that often characterize waters inhabited by sago.

Maximum photosynthetic rate for sago is 2.1 μmol O_2/mg chlorophyll per minute. This rate is maximum at pH < 7.0 at dissolved inorganic carbon concentrations found in nature, but photosynthesis can continue to pH > 10.0 (Sand-Jensen 1983). Gross (1.2 mg O_2/L/h) and net (0.98 mg O_2/L/h) primary productivity of a sago community in a eutrophic Wisconsin stream peaked at 1000 h; maximum respiration was 0.65 mg O_2/L/h (Madsen et al. 1988). Azcon-Bieto et al. (1987) measured the dark respiration rate of sago leaves (39.4 μmol O_2/g dry weight

per hour) and stems (13.3 μmol O_2/g dry weight per hour) and found it markedly lower than for several other submersed angiosperms, bryophytes, and algae common to temperate climates. This could help explain sago's success in polluted, oxygen-poor environments. Jana and Choudhuri (1979, 1981, 1982a) reported that the dark respiration rate and photorespiration rate of sago is high, but apparent photosynthesis is low. Thus, the authors postulated that sago is not able to compete in tropical or subtropical waters inhabited by plants with less photorespiratory O_2 demand.

Madsen (1986) found sago to have a rather modest photosynthetic rate, comparable to other *Potamogetons*, but much less than for one of sago's most common associates and likely competitor, *Myriophyllum spicatum*. He concluded that although sago does not exhibit the high photosynthetic rates of species common to warm waters, the plant is successful because it can exploit the environment early in the growing season, before plants with higher rates are at an advantage. He also noted that sago has other morphological and reproductive features that assure the plant success in various aquatic habitats. Westlake (1967) also found sago to have low photosynthetic capacity.

Sago grown from turions in N-deficient medium for 35 days was only slightly paler than control plants, but control plants averaged 10 cm longer (Devlin and Yaklich 1971). During the same experiment, P-deficient plants were similar to controls in both height and dry weight.

Ca deficiency in sago is evidenced by reduced growth; rapid paling of leaves followed by necrotic spotting, curvature, and eventual gelatinous texture; and weakening after 19 days of initial growth from turions. This is attributed to the function of Ca as a [strengthening?] constituent of cell walls in the form of calcium pectate (Devlin et al. 1972).

After 20 days of initial growth, Mg deficiency in sago grown from turions is evidenced by reduced weight and slight chlorosis; this reflects the function of Mg in the chlorophyll molecule (Devlin et al. 1972).

Potassium deficiency in sago caused reduced growth, a darker green color, and shortened internodes (Devlin et al. 1972).

Experiments of Peter et al. (1979) documented the upward translocation of copper in sago, from sediments to stem apices and youngest leaves; similar translocation of lead did not occur. Jana and Choudhuri (1979, 1981, 1982a) found that cadmium, Cu, and mercury increased signs of photorespiration in sago, whereas Pb decreased them. Everard and Denny (1985) discovered that sago does not absorb Pb as fast as several other submersed and floating macrophytes; they attributed this to sago's relatively thick cuticle. Marchyulenene et al. (1978) measured uptake of nuclides of Pb and strontium in sago but did not investigate toxic effects.

In young sago plants grown from turions, chlorophyll a and b content peaked when temperatures were held at 30°C, but carotenoids reached maximum values when plants were held at 17°C (Spencer 1986a). Spencer postulated that the protection afforded the chlorophyll by the carotenoids at low temperatures can indicate an adaptation of sago for early growth in cooler water. Spencer and Anderson (1987) found little difference in chlorophyll a or carotenoid content in sago cultured under photoperiods of 10, 12, or 14 h, but these pigments were reduced in plants grown at a 16-h photoperiod.

Heavy flow of carbohydrates from turions to upper parts of the young plants occurs during the first 2–3 weeks of growth (Hodgson 1966). The relative growth rate of sago and root-to-shoot ratio was not significantly affected by photoperiod, but production of turions was enhanced at photoperiods up to 12 h (Spencer and Anderson 1987).

Jana and Choudhuri's (1982b) study of ethylene production in sago revealed that it may be geared to rapid senescence when compared to several other hydrophytes. These authors (1987) also tested the ability of various antioxidants to arrest senescence in sago leaves and found glutathione most effective.

Lakes with an abundance of rooted hydrophytes can contain substances that inhibit the growth of phytoplankton regardless of nutrient supply, illumination, or water temperature (Hogetsu et al. 1960), but the source or composition of such substances remain unknown. Substances that increase turion growth and inhibit germination in seeds of other plants can be distilled from sago turions (Yeo 1965), but it is unknown whether these substances function in nature.

Growth and Production

Rate

Vegetation

Growth rate of plants is often measured by the speed at which carbon is accumulated per unit of

plant weight or inhabited area. Wallentinus (1979) considered sago in a group of plants of low production rate (<2 mg C/g dry weight per hour) when compared with several other species of vascular plants and many algal taxa of thalassic waters. Brooker and Edwards (1973), Jupp and Spence (1977b), and Kvet and Husak (1978) found that sago accumulated C at 548–1,400 mg/m^2/day. Peak rates of 0.06 mg C/m^2/s occur for short periods in fertile streams (Peverly 1985). Huebert and Gorham (1983) noted a seasonal periodicity in sago biomass production under standardized laboratory conditions, suggesting an internal regulation independent of obvious external signals.

Productivity is also measured by increases in weight over time. Laboratory cultures by Sheldon (1987) indicated that sago was intermediate in dry weight gain per unit of time when compared with 13 other submersed macrophytes commonly found in Minnesota lakes. Ozimek et al. (1986) found that sago in polluted and unpolluted sites in a Polish lake increased dry weight fastest early in the season, but that plants from polluted sites reached peak weight in July, whereas those from unpolluted sites continued to gain weight until October. Plants from unpolluted sites usually allocated more biomass to underground parts than plants found in polluted sites.

Sago was producing a maximum of 5.2 g/m^2/day (dry weight) in early July and 2.3 g/m^2/day in mid-August at time of greatest standing biomass in a fertile North Dakota wetland (Kollman and Wali 1976). Peterka and Hanson (1978) found similar (about 3.4 g/m^2/day) growth rates among young sago planted in pans placed in waters obtained from a fertile North Dakota river.

Howard-Williams (1978) found that sago produced at most nearly 16 g/m^2/day during the rapid branching period in February in a South African wetland; he considered this exceptionally high for any submersed hydrophyte. Purohit (1981) recorded a maximum incremental growth rate of 16.6 g/m^2/day in a fertile Indian wetland. The aboveground portions of plants grown from turions added up to 223 mg/day oven-dry weight during the first 35 days and 220 mg/day during the first 21 days in the culture experiments of Otto and Enger (1960) and Ryan and Riemer (1975), respectively. An average plant cultured by Teeter (1963, 1965) added 12 mg dry weight per day during growth days 42–63.

Shoots from turions grew 0.4–0.7 cm/day over the first 10–11 days and 1.2 cm/day over the first 20 days while gaining 29 mg/day wet weight (Frank and Hodgson 1964; Devlin et al. 1972). Plants cultured from turions by Devlin and Yaklich (1971) grew 1.27 cm/day and added 3.4 mg/day dry weight.

Photoperiods from 10 to 16 h seem to have little effect on weight of cultured sago plants up to at least 8 weeks old (Spencer and Anderson 1987). Sago plants increase faster in length but slower in fresh weight under lower light intensities (Devlin and Karczmarczyk 1975). Plants grown from turions grew 2.16 cm/day for 21 days (Ryan and Riemer 1975), and young plants raised outdoors by Peterka and Hanson (1978) grew 1.2 cm/day for 45 days. Culture experiments of Spencer (1986a) showed that, at optimum growth temperatures (23–30° C), low light intensities stimulate shoot elongation, but leaf length increases with increasing temperatures at all irradiances. Plants cultured by Otto and Enger (1960) elongated ≤1.75 cm/day for 42 days in 800 ppm sediment concentrations, but they showed much slower growth in less turbid water. Purohit (1981) recorded growth of up to 13 cm/day for sago in deep (4.5–5.5 m) water when water levels were increasing.

Sago thus seems perfectly adapted to begin growth early in cool, dimly lit waters. This alone could explain sago's great success in temperate climates. The plant can also grow rapidly when water levels are rising and so is adapted to subtropical wetlands subject to monsoons as well as temperate wetlands where the greatest increases in water levels usually coincide with spring runoff and the beginning of the growing season.

Propagules

Teeter (1963, 1965) found, through culture experiments, that during growth days 42–63, sago turions gained 3.8 mg/day dry weight and by 63 days an average plant had 7 turions, 10.6 rhizome shoots, and 0.7 drupelet spikes. He also showed that plants added 0.44 rhizome shoots per day from day 63 to day 91. In culture, sago turions can form in as little as 4 weeks, and by 8 weeks individual plants can have >12 turions which can compose 38% of plant dry weight (Spencer and Anderson 1987).

Ozimek et al. (1986) showed that young (small) turions germinate very quickly, but that the plants grown from them add weight to both above- and belowground parts at a much smaller monthly rate than do plants cultured from old (large) turions. They also observed that, compared with plants grown from old turions, plants grown from young turions

added weight to belowground plant parts at a much faster monthly rate than to aboveground parts.

Yield

Vegetation

Sago forms dense monotypic stands of up to 840 individual plants per square meter or 1,000 shoots per square meter (Sheldon and Boylen 1977; Howard-Williams 1981; Purohit 1981). Plants from densest aggregations at eutrophic sites in a Polish lake formed 100 shoots per square meter where total above- and belowground biomass was 43.6 g/m^2 dry weight (Ozimek et al. 1986). Greatest sago biomasses (>1,500 g/m^2 dry weight) were found in Africa (Zaky 1960; Aleem and Samaan 1969b; Howard-Williams 1978; Appendix A).

Although some leaves are naturally abscissed or weight is otherwise lost during the growing season, seasonal maximum biomass of sago (B_{max}) is not much less than total annual production (P). P/B_{max} ratios typically are between 1.1 (Purohit 1981; Berendsen and Van der Kruis 1986, cited in Van Wijk 1988) and 1.3 (Howard-Williams 1978), although these likely were slightly underestimated because of the methods used (Carpenter 1980). Madsen (1986) considered P/B_{max} ratios >2.0 reasonable for streams or areas of heavy wave action.

In nature, the belowground biomass of sago can vary from 4% to 78% of total plant weight (Howard-Williams 1981; Kautsky 1987; Van Wijk 1988). The proportions of plant weight found above and below ground at various times during the year depend greatly on whether the habitat creates conditions suitable for the perennial or annual life cycle of sago and whether or not the site is grazed (Van Wijk 1988). Culture experiments of Teeter (1963, 1965) showed that turions alone can make up 17% of the total weight of 9-week-old plants.

Ozimek et al. (1986) noted that heavier sago plants seemed to allocate less biomass to underground parts than lighter plants in mesotrophic to hypereutrophic waters. They found as little as 3.0% or as much as 41.4% of the dry weight of sago below ground. Kautsky (1987) observed that aboveground sago biomass can vary from 96% of total plant weight on soft bottoms in sheltered sites to 76% on exposed sands and gravels.

Madsen (1986), working in a polluted Wisconsin stream, found variance of sago shoot biomass nominal until the maximum was attained and flowering occurred. After that, senescence began and biomass varied greatly for the rest of the growing season, as clones of overlying shoots sequentially flowered and senesced.

Maximum standing crop or total biomass of sago <200 g/m^2 dry weight might indicate the presence of several factors that limit growth (Appendix A). However, reproductive strategy may also be important in this regard—of 11 sago-dominated European wetlands studied by Van Wijk (1988), the 5 with the highest peak biomass had sago populations that exhibited a perennial life cycle, with both vegetative parts and propagules surviving winter and contributing to biomass production over a relatively long growing season.

Propagules

Propagule densities and yields under various field conditions are shown in Table 2. Direct comparisons between studies are unwarranted because environmental conditions and genetic populations differ greatly. Comparisons within studies are also subject to some error, as where waterfowl exclosures result in greater organic matter inside because of reduced wave action. Nevertheless, likely factors resulting in high turion production are sparse carp and waterfowl populations, brackish or oligosaline water salinity, and maintenence of sufficient water depth during the growing season. These factors, as well as adequate protection from wave action, also seem to result in greater drupelet production.

Mean turion densities in California irrigation canals were 0.2–4.1 per 100 cm^3, and the densities were not significantly related to the depth of sediment where the turions were collected (Spencer 1987). The U.S. Bureau of Reclamation (Garrison Diversion Unit Refuge Monitoring Annual Report 1987, unpublished) found little relation between turion density and depth or sediment characteristics on various water bodies along the James River, North Dakota and South Dakota, and concluded that both factors needed to be looked at simultaneously before their effects could be understood.

Propagule production from single sago propagules can be astounding. In a single-season culture experiment, Yeo (1965) grew 36,000 subterranean turions, 800 axillary turions, and 6,000 drupelets from 1 turion and 63,300 drupelets, and 15,000 subterranean turions from a single drupelet. Densities reached during this experiment were 3,308 subterranean turions per square meter from a single turion and 8,624 drupelets per square meter from a single drupelet. In nature, wind drift can deposit

Table 2. *Density and yield (dry wt)*[a] *of sago pondweed (*Potamogeton pectinatus *L.) propagules under various conditions.*

Turions		Drupelets			
Density (no./m^2)	Yield (g/m^2)	Density (no./m^2)	Yield (g/m^2)	Conditions	Reference[b]
387		1,960		After dewatering and carp removal	1
1,033	21.5			Waterfowl and carp present	2
4,909	102			Waterfowl and carp excluded	2
92	4.0			Clay loam substrates	2
59	1.2			Silt substrates	2
12	0.2			Sand substrates	2
		1,615	2.9	Salinity 0.84–1.9 g/L	2
		few		Salinity 7.2–8.25 g/L	2
		2,180	4.0	Depth 41–46 cm	2
		403	0.73	Depth <8 cm	2
464				Open to waterfowl	3
688				Waterfowl excluded	3
2,390	450			Open to waterfowl	4
192				Mesotrophic	5
100				Eutrophic	5
48				Eutrophic, polluted	5
52				Eutrophic, unpolluted	5
8				Hypereutrophic	5
115		181		Exposed sands	6
45		455		Sheltered muds	6
	6.4		0.85	Carp excluded	7
few			7.2	Turbid, carp present	8
	103			Waterfowl excluded	9
	44			Open to waterfowl	9
629	60	302	1.2	Sheltered, brackish	10
337	22		0.04	Exposed, brackish	10
440	11	20	0.11	Exposed, fresh	10
888	37		0.07	Exposed, fresh—slightly brackish, open to waterfowl	10
1,784	110	363	5.3	Exposed, fresh—slightly brackish closed to waterfowl	10
759	13	0	0	Fresh running water	10
750	7	0	0	Fresh running water	10
	69			Fresh running water	11
3,975	200	651	2.9	Oligosaline, rising summer water levels, sheltered	10
1,330	86	806	3.4	Oligosaline, falling summer water levels, sheltered	10
467	28	1,019	5.8	Oligosaline, 30–45 cm depth, much wave action	10
495	22	3,707	20.4	Oligosaline, 40–70 cm depth, moderate wave action	10

[a] Fresh (wet) weight yields were multiplied by 0.13 to obtain dry weight; data from Van Wijk (1988) were used to convert ash-free dry weight yields for turions and drupelets to dry weight by multiplying by 1.12 and 1.16, respectively.

[b] 1 = Lutz 1960; 2 = Craner 1964; 3 = Jupp and Spence 1977b; 4 = Jarvis et al. 1985; 5 = Ozimek et al. 1986; 6 = Kautsky 1987; 7 = Sterling 1970; 8 = Rich 1966; 9 = Anderson and Low 1976; 10 = Van Wijk 1988; 11 = Madsen 1986.

>4,000 drupelets per square meter on bottoms away from areas of greatest sago production (Aleem and Samaan 1969b).

Chemical and Caloric Content

Vegetation

Dry matter constitutes 7.0–16.7% of the fresh weight of sago (Edwards and Owens 1960; Oborn 1964; Hannan and Dorris 1970; Paullin 1973; Purohit 1981; Chapman et al. 1987). Penuelas et al. (1988) reported that the dry weight of leaves was 11.8% of fresh weight and that of stems was 13.6%; this was markedly higher than for several other submersed angiosperms. Purohit (1981) found that highest dry matter content existed in sago at time of peak biomass. Air-dried sago is about 92.8% dry matter (Linn et al. 1975).

Ash content varies widely (10.3–56% of dry weight; Rich 1966; Hannan and Dorris 1970; Sugden 1973; Kollman and Wali 1976; Kvet and Husak 1978; Katanskaya 1986; Petrova 1986). Ash content is directly related to marl encrustations at time of collection, and levels depend greatly on treatment of the collected material (Westlake 1965; Kollman and Wali 1976; Petrova 1986). Data compiled by Katanskaya (1986) suggest that ash content in sago rises with increases in water salinity and total hardness.

Organic matter composes about 83% of the oven-dry weight of cultured sago shoots (Huebert and Gorham 1983) and 58–90% of material gathered in nature (Carpenter 1980; Purohit 1981; Katanskaya 1986). Organic C content is about 30–39% of dry weight (Owens and Edwards 1962; Hannan and Dorris 1970; Neel et al. 1973; Hill 1979) and 48% of the ash-free dry weight (Edwards and Owens 1960).

As percent dry weight, the aboveground biomass of whole sago plants or sago foliage contains 10.2–17.1% protein, 14.7–40.3% crude fiber, 0.5–2.7% crude fat, and 16.1–57.8% soluble carbohydrates (Sugden 1973; Linn et al. 1975; Anderson and Low 1976). Paullin (1973) compared the nutritional qualities of sago with seven other submersed vascular hydrophytes and found that sago was lowest in protein and fat. Sugden (1973) listed 17 amino compounds found in sago foliage. Linn et al. (1975) analyzed fiber from sago and found that it contained 51% neutral detergent fiber, 42% acid detergent fiber, and 6% acid detergent lignin.

Caloric content of the aboveground parts of sago is 2.0–3.7 Kcal/g ash-free dry weight, and likely is greatest in tissue 3 weeks old (Sugden 1973; Kollman and Wali 1976; Handoo et al. 1988). Handoo et al. (1988) found that the caloric content of sago was slightly lower than the mean for seven other submersed macrophytes tested. In subtropical climates, whole plants can have up to 4.7 Kcal/g ash-free dry weight at time of fruiting, but another, smaller peak occurs in winter when plants are known to accumulate more lipids (Purohit 1981).

Comparison of the elemental composition of sago (Table 3) with data presented by Hutchinson (1975) indicated that the plant is higher in Ca, iron, K, lithium, Mg, Na, and several micronutrients than the average hydrophyte. However, the higher values

Table 3. *Elemental composition of aboveground green tissues of sago pondweed.*

Element	Unit of measure[a]	Range or single observation (reference[b])
Aluminum (Al)	ppm	400 (1)–2,700 (2)
Barium (B)	ppm	170 (3)
Carbon (C)	%	35.7–39.5 (4)
Calcium (Ca)	%	0.16 (5)–22 (1)
Cadmium (Cd)	ppm	3–26 (6)
Chlorine (Cl)	%	0.55–2.35 (7)
Cobalt (Co)	ppm	2.8 (8)–26.0 (4)
Copper (Cu)	ppm	8 (8)–103 (3)
Iron (Fe)	%	0.03 (5)–5.0 (1)
Hydrogen (H)	%	5.2–5.7 (4)
Potassium (K)	%	0.59 (1)–5.34 (5)
Lithium (Li)	ppm	13–25 (1)
Magnesium (Mg)	%	0.05 (9)–6.08 (1)
Manganese (Mn)	%	0.01–0.53 (5)
Molybdenum (Mo)	ppm	<65–<110 (4)
Nitrogen (N)	%	1.24 (5)–6.01 (10)
Sodium (Na)	%	0.10 (9)–4.00 (5)
Nickel (Ni)	ppm	9–21 (1)
Phosphorus (P)	%	0.07 (11)–1.11 (5)
Silicon (Si)	%	0.5–1.05 (1)
Strontium (Sr)	ppm	120–530 (1)
Vanadium (Va)	ppm	1,650 (12)
Zinc (Zn)	ppm	12 (1)–340 (6)

[a]Measurements refer to oven-dry matter in whole plants or various tissues, except Va, which refers to ash. High levels of Ca, Fe, and Mg likely are caused by external encrustations.
[b]Reference: (1) Kollman and Wali 1976; (2) Peverly 1985; (3) Adams et al. 1973; (4) Neel et al. 1973; (5) Van Vierssen 1982b; (6) Adams et al. 1980; (7) Ozimek 1978; (8) Varenko and Chuiko 1971, cited in Hutchinson 1975; (9) Riemer and Toth 1968; (10) Ho 1979; (11) Howard-Williams 1981; (12) Petkova and Lubyanov 1969, cited in Hutchinson 1975.

could merely be related to external carbonate encrustations that are often included in analyses (Kelly and Ehlmann 1980). Ho (1979) found that concentrations of Ca and Mg in sago tissue were negatively correlated with amounts of these two elements in the water column, and attributed this to the formation of carbonate encrustations on the plants. Encrustations could also have caused seasonal lows in these elements in sago tissue—lows that occurred around the time of peak sago biomass in a polluted Wisconsin stream (Madsen 1986). Gopal and Kulshreshtha (1980) calculated that a 1-m² bed of sago at peak biomass would contain 27 g of Ca, 9.6 g of Mg, 27 g of N, and 0.7 g of P.

Kollman and Wali (1976) found that Na, K, and C content in sago tissue rose during the rapid growth period, declined during reproduction, and rose again during plant decline in a mixosaline, relatively unpolluted North Dakota lake. Amounts of Fe and Mg peaked at the end of the reproductive period. Many other elements (aluminum, Ca, Cu, nickel, silicon, Sr, zinc) increased during the fruiting period and decreased thereafter. Concentrations of manganese remained fairly constant until the decomposition period when an increase occurred. Complex interactions among plant uptake from sediments and water column, marl formation and disintegration, hydrology, and the ecosystem made it impossible to attribute these trends to any single factor. Hill (1979) found that N content of sago in a Minnesota lake reached maximum in late May, whereas organic C and P content peaked in mid-June.

Ho (1979) sampled sago shoots during their period of maximum growth in a lake heavily polluted with domestic sewage and found increasing concentrations of Ca, P, and Mg and decreasing levels of N. Potassium and sodium attained minima and maxima, respectively, during the middle of the period, while Fe levels initially fell and then stabilized. Significant positive correlations were found between tissue N and concentrations of inorganic N in the water column and between tissue P and PO_4 content of the water. Levels of N and P in sago can be well above that required for growth, indicating the presence of luxury consumption (Jupp and Spence 1977b; Ho 1979; Madsen 1986).

Sago can play an important role in the P cycle in wetlands (Vermaak et al. 1981; Huebert and Gorham 1983) and release P into the water column (Vermaak et al. 1976). Howard-Williams (1981) found

that dense stands of sago can remove large amounts of N and P from the water column in a single day. Vermaak et al. (1976) cultured sago in relatively high (0.3 mg/L) PO_4–P concentrations and found that, within 5 days, the plants had concentrated P^{32} to 4,738 times the amount found in the water column. This was more than several other submersed, emersed, and free-floating hydrophytes, but only 10% of that found for the filamentous alga *Oedogonium*.

Purohit (1981) measured highest Ca content (12.46%) in sago from sites where productivity was greatest, highest total N content (4.29%) where productivity was lower than average, and highest total P content (0.215%) when biomass was declining.

Ozimek (1978) related the chemical content of sago to the degree of pollution from municipal sewage and found that, as loadings increased, chlorine, Fe, Mg, Na, and Zn concentrations in plants increased and Ca and K decreased, whereas Mn, N, and P remained nearly constant. One variety of sago (var. *scoparius*) was only found in the most heavily polluted site and was the only vascular plant present.

Madsen (1986) measured changes in the concentrations of major and minor nutrients in sago tissue collected during the growing season in a polluted stream. Peak N, K, and S concentrations tended to occur near times of peak sago biomass, whereas the opposite was true for Ca, Mg, Zn, and Cu. Manganese and boron tended to increase during the growing season, whereas concentrations of P, Fe, Na, and Al varied greatly. None of these elements except K was found below critical concentrations, and the brief period of low indicated K could have been caused by acid-washing during analysis. The author concluded that there was no limitation to macrophyte growth in this stream attributable to lack of nutrients and that water column loadings alone were more than adequate to prevent nutrient limitation to the growth of sago and other submersed macrophytes.

In natural waters, greater concentrations of N and P have been found in the upper or aboveground parts of sago than in the lower or belowground portions (Neel et al. 1973; Van Vierssen 1982b). Leaves were highest and rhizomes lowest in concentrations of both N and P in unfertilized plants studied by Howard-Williams (1981); roots concentrated N slightly more than did stems, but the difference between P in stems and roots was negligible. He found that treating the water column with extra heavy

amounts of N and P would raise the concentrations of these elements in the four plant organs. Getsinger et al. (1982) found greater N and P concentrations in sago roots than in shoots in a wetland with low ambient P. Combined data of Neel et al. (1973), Getsinger et al. (1982), Van Vierssen (1982b), and Peverly (1985) indicate that Al, Ca, Mg, and Mn are more concentrated in upper or aboveground tissue than in lower or belowground tissue, whereas the reverse is true for cobalt, Cu, K, and molybdenum. Inconclusive results were found for Fe, Na, and Zn.

Propagules

Turions contain slightly higher amounts of protein and much more carbohydrate than sago foliage, but turions are much lower in fiber and ash (Anderson and Low 1976). Hodgson (1966) found that the high (74% of dry weight) carbohydrate reserves in cultured turions were exhausted 16–23 days after growth began and that the proportion of starch to sugar was greater in larger turions. He found sucrose only in unsprouted turions and sprouted turions up to 10 days old, but older turions from growing plants also contained some fructose and glucose.

Drupelet heads contain large amounts of fat (6.3–6.9% dry weight) compared to foliage (0.5–2.7%) or turions (0.9–1.1%; Anderson and Low 1976).

In summary, sago is able to greatly concentrate major nutrients, micro-nutrients, and trace elements (Table 3) as well as profoundly influence the nutrient flux in natural waters. Whether this ability is caused by a propensity to form external encrustations or, for major nutrients, to exhibit luxury consumption remains unclear. The large carbohydrate accumulation by sago turions undoubtedly explains their extensive use by migrant and wintering waterfowl.

The high uptake capacity of mineral elements by sago and other hydrophytes has led to proposals for the use of such plants in tertiary waste treatment for nutrient and waste removal from domestic or industrial effluents (Dykyjova 1979) or to reduce nutrient pollution in fairly large water bodies (Howard-Williams 1981). However, comparable numerical data on mineral uptake and fluxes are still largely unavailable because there remain many sources of error in analyses of plant tissue composition and much unexplained variability in chemical composition in plants because of plant age, phenology, and ecotype (Dykyjova 1979).

Decomposition

Senescence in sago begins shortly after flowering and proceeds as clones flower and die, which exposes clones not in the canopy that, in turn, flower and die (Madsen 1986). In fall, part of the upright stems of sago detach and are washed ashore; remaining senescent stands collapse gradually and decompose on the bottom (Verhoeven 1980a). In some lakes, tons of sago decompose on shore as stems and leaves wash up after being discarded by feeding waterfowl.

Peak sago biomass in a polluted Wisconsin stream occurred after 113 days and senescence began around the end of July (Madsen 1986). After a 129-day growing season, the entire sago community in a North Dakota lake was senescent by 6 October (Kollman and Wali 1976).

Sago decomposes rapidly at old age (158 days in a South African wetland), and the decay products form a rich food for benthic filter-feeding animals (Putschog 1973; Howard-Williams and Davies 1979). Howard-Williams and Davies (1979) showed that nearly all K is lost from decomposing sago within a week but that N and P losses are much slower. Litter bag experiments of Byren and Davies (1986) in another South African wetland showed how important shredding and grazing invertebrates were for increasing surface area for microbial colonization and attack of sago. They estimated complete decomposition in 145 days; listed the animals that dominated the litter bag fauna; graphed the changes in ash, N, and P content of the plant material; and provided micrographs showing changes in microorganisms with time. Indian sago in closed containers decomposed 44% in 60 days (Kulshreshtha and Gopal 1980) and, in large-mesh bags, decomposed completely in 56 days in summer (Purohit 1981).

Decomposition caused by microbes probably is hastened by cuticular damage from periphyton (Howard-Williams et al. 1978). When decaying sago plants react with oxygen, the oxygen depletion and formation of carbon dioxide causes complex chemical changes in the water column and sediments. Calcareous incrustations flake from the leaves, many ions are reduced to more soluble forms, and hydrogen sulfide and several insoluble metallic sulfides are formed (Kollman and Wali 1976).

Habitat

Wetland Type

Sago normally occurs in water bodies or those portions where water is permanently present (Mirashi 1954; Verhoeven 1980a; Grillas and Duncan 1986) or absent for no more than 1 to 3 months (Coetzer 1987.) Stream environments favor linear-leaved species like sago that tend to grow from the base (Madsen 1986), but Pip (1987) found no significant tendencies for sago to occur more frequently in either lentic or lotic habitats. Sago occurs in the estuarine, riverine, lacustrine, and palustrine wetland systems of Cowardin et al. (1979). Under this classification scheme, sago is a dominance type in the class Aquatic Bed in wetlands with subtidal and irregularly exposed water regimes in estuarine systems; in tidally-influenced riverine systems, sago occupies permanently flooded and intermittently exposed sites. In inland systems, sago variously grows in wetlands with permanently flooded, intermittently exposed, semipermanently flooded, or artificially flooded water regimes.

In a wetland classification system developed specifically for basins in the glaciated prairie region of North America (Stewart and Kantrud 1971), sago is restricted to the deep marsh zone of permanent and semipermanent ponds and lakes. Sago occasionally occurs in seasonal (Stewart and Kantrud 1971) wetlands if surface water is continuously present for more than 3 years, and the presence of sago in these wetlands suggests that they have experienced, or can be expected to experience, several years of continuous flooding (Millar 1973). Sago became well established when formerly dry sites in Utah were continuously flooded to a depth of 30 cm for 2 years (Nelson 1954). Sago reaches peak frequency in the regenerating and degenerating phases of prairie wetlands defined by Van der Valk and Davis (1978). The former phase occurs just after basins refill; the latter, just before a variety of agents causes a rapid decline in emergent hydrophytes.

Wetland Area and Fetch

When water depths decrease to 0.5 wavelengths, waves begin to feel the bottom and release energy, and larger, more damaging waves are caused by increased wind and fetch (Bird 1968). The depth of the wave-mixed zone is an important factor that determines the depth of water colonizable by macrophytes. The extent of this zone depends on shore slope and aspect in relation to prevailing winds and lake size (Spence 1982). In shallow wetlands, the wave-mixed zone can largely coincide with the macrophyte zone, but if fetches are large, the wave-mixed zone deepens and the effects of wave action on sediment-induced turbidity can prevent growth of sago and other submersed macrophytes (Chamberlain 1948; Spence 1982) or wash plants out of fine-textured bottoms (Carter et al. 1985a).

The data of Anderson and Jones (1976) show that the macrophyte zone in shallow lakes larger than about 500 ha normally occupies <25% of the lake area. Anderson (1978) was able to predict, with a combination of four maximum tolerance values, the presence or absence of sago in 136 of 140 sample sites in a large Manitoba wetland. No sites with a maximum fetch of 2,300 m, north fetch >600 m, northwest fetch >500 m, and water depth >120 cm supported sago. Lake Ichkeul in Tunisia (90 km^2) supports about 20 km^2 of sago (Skinner and Smart 1984), but the plant is absent or sparse in the central area and along several long stretches of shoreline, possibly because of excessive fetch. Kantrud (1986a) found a similar absence of sago in the central area of maximum fetch in a large (1,132 ha), shallow North Dakota wetland. Ongoing studies of Butler and Hanson (1985, 1986, 1988, unpublished) show that in a large (1,598 ha), shallow (mostly <4 m) Minnesota lake, concentrations of suspended solids are much greater (40–100 ppm) in central areas of greater fetch than in deeper, more sheltered sites (10–50 ppm). They used the formulas of Carper and Bachman (1984) to show that even moderate winds could expose large areas of the bottom to wind energy sufficient to cause sediment resuspension and increased turbidity. On large lakes, littoral zones can be barren due to wave action, with sago and other macrophytes restricted to river inlets (Sheffer and Robinson 1939). In other large lakes, wave action can restrict sago beds to deeper (>3–4 m) sites where plants grow in sparse clumps (Hill et al. 1975). Pip (1987) observed no significant differences in frequency of sago in wetlands larger or smaller than 10 ha in area.

Water Column

Depth

Worldwide, sago has been found growing in a variety of substrates—from wet mud to under waters

10 m deep; optimum or luxurious growth has been observed in waters 7.0 cm–6.0 m deep (Table 4). Turbidity determines depth distribution because optimum growth has not been observed in moderately turbid water deeper than 2.0 m or in highly turbid water deeper than 0.9 m. Distribution according to depth seems unrelated to water chemistry but strongly related to bottom texture. Optimum growth has not been recorded with clay or silt bottoms under water >1.5 m deep. Conversely, optimum growth has been noted on sand, mud, or marl bottoms at depths >2.0 m. The water column above fine-textured bottoms is, of course, subject to greater wind-induced turbidity than that above coarse-textured bottoms. Water pressure, rather than insufficient light, may limit the distribution of sago on the Canadian prairies to waters <8 m deep (Hammer and Heseltine 1988).

Anderson and Low (1976) found that a highly significant regression of sago standing crop was a quadratic function of water depth in controlled plots in a Manitoba wetland, and the results agreed closely with field observations (Anderson 1978). Robel (1961b, 1962) also showed that peak sago biomass occurred over a narrow range of depths in managed Utah wetlands. Craner (1964) determined that biomass of sago vegetation and drupelet heads—but not turions—showed significant positive correlations with water depth. He found that best vegetative growth and greatest density of drupelet heads was at depths of 30–69 cm and 41–46 cm, respectively. Haag (1983) found that the greatest number of sago seedlings were at the shallowest sites in an Alberta lake, but seedling numbers were not significantly related to depth. He noted that sexual reproduction at such sites is often limited by insufficient light, short growing period, lack of nutrients, and absence of adequate protection from wave action.

Discontinuities in the depth distribution of sago within a wetland can be a result of wave action. In an African lake, sago did not occur at depths <3.5 m except in sheltered areas, where plants grew at depths <2.0 m (Boltt et al. 1969). Bimodal depth distribution of sago also can be caused by potential competitors. Denny (1972) found that peak (≥50%) sago frequencies were at 0.75–1.5 m and 3.5–3.75 m in a silty, clay-bottomed African lake, with the depth zone between (1.5–3.5 m) dominated by *Chara* sp. Two zones of sago were present in a sandy-bottomed African wetland studied by Taylor (1983). A shoreward zone in about 0.6 m water was separated from a lakeward zone in about 1.0 m water by a 40-m-wide zone of sparse *Chara*. The data of Gibbs (1973) suggest that the often seen cycles of phytoplankton-macrophyte dominance can be a function of water depth, the competitive advantage being with the phytoplankton in deeper wetlands.

The depth distribution of sago can also change with season. Purohit (1981) recorded maximum sago density of 840 plants per square meter at a depth of 0.5–1.5 m where plants persisted for 9 months, whereas at 2.5–3.5 m, plants reached a density of only 490/m^2 but persisted for 11 months. Voge (1987) found sago at depths up to 5 m in early summer, but by mid-summer no plants were found at >3 m.

Table 4. *General habitat features for sago pondweed occurrences arranged according to increasing observed tolerance of water depth.*

Depth (m)					
Range or single observation	Optimum[a]	Water turbidity	Water salinity	Predominant substrate texture	Reference
0.23			mixosaline	organic muck	Wrubleski and Roback 1987
0.25					Kiorboe 1980
0.2–0.3		little	mixosaline	clay loam	Nelson 1954
0.2–0.3					Ellis 1955
<0.35		limiting	fresh		Andersen 1976
0.12–0.38	0.25		mixosaline	clay	Sterling 1970
0.3–0.4		limiting	mixosaline		Verhoeven 1980a
0.4				organic mud	Verhoeven 1980a
0.07–0.5	0.4–0.45	limiting	mixosaline	clay	Robel 1961, 1962
	0.46	limiting		silty marl	Rich 1966

Table 4. *Continued.*

Depth (m)		Water turbidity	Water salinity	Predominant substrate texture	Reference
Range or single observation	Optimum[a]				
0.05–0.5				clay	Verhoeven 1980a
	0.2–0.5		mixosaline	sandy clay	Jensen 1940
	0.3–0.6			muddy sand	Tryon 1954
0.45–0.60				silt	Peltier and Welch 1969
	0.07–0.64			muck	Smeins 1965
<0.08–0.69	0.30–0.69		mixosaline	silt, clay loam	Craner 1964
	0.6–0.7	limiting	mixosaline	sand-silt-loam	Sincock 1965
<0.7		limiting	fresh		Congdon and McComb 1976
0.2–0.7			mixosaline	mud, organic, clay	Meriaux 1978
0.28–0.71		moderate	mixosaline	sand	Gibbs 1973
0.25–0.75			fresh	gravel, sand	Olsen 1950
	0.6–0.75		mixosaline		Shubert 1982
	0.6–0.75		mixosaline	sand-silt	Kollman and Wali 1976
<0.76				gravel-rubble	Huber 1952
<0.8			fresh		Swindale and Curtis 1957
>0.8					Haslam 1978
>0.8			fresh	mud	Brooker and Edwards 1973
0.27–0.81				sand, gravel	Madsen 1986
0.1–0.85	0.8–0.85		mixosaline	gravel, sandy mud	Verhoeven and Van Vierssen 1978a
0.74–0.89			mixosaline		Madsen et al. 1988
<0.9		limiting		mud	Bourn 1932
	≤0.9	limiting		silt	Logan 1975
0.3–0.9				clay	Lathwell et al. 1969
0.7–0.9			mixosaline	mud	Klavestad 1957
	0.8–0.9	moderate		silt	Jackson and Starrett 1959
0.30–0.91	0.30–0.61			muck	Sharp 1939
0.61–0.91				muck, sand	Threinen and Helm 1954
0.69–0.91	0.78			sludge	Westlake 1961
0.28–0.93	0.51	moderate	mixosaline	silt, sand	Olson 1979
0.2–1.0				peat	Kohler et al. 1971
0.3–1.0	0.6–0.7				Anderson 1978
0.5–1.0			mixosaline		Mathiesen and Nielsen 1956
0.7–1.0			fresh	sand	Bernatowicz and Zachwieja 1966
	<1.0			marl	Nichols and Mori 1971
<1.0			mixosaline	sand	Evans 1953
<1.0			mixosaline		Verhoeven and Van Vierssen 1978b
<1.0				clay	Jupp and Spence 1977a
<1.0			mixosaline		Gerbeaux and Ward 1986
≤1.0					Kuflikowski 1977
1.0			mixosaline	mud	Aleem and Samaan 1969a
	1.0			silt, sand	Van der Valk and Bliss 1971
0.03–1.2	0.35–1.0	moderate	mixosaline	clay	H. A. Kantrud, personal observation
0.15–1.2				muck, silt	McDonald 1951
	0.3–1.2			sand, organic	Moyle and Hotchkiss 1945
0.3–1.2					Titcomb 1923

Table 4. *Continued.*

Depth (m)					
Range or single observation	Optimum[a]	Water turbidity	Water salinity	Predominant substrate texture	Reference
0.5–1.2	0.5–1.0				Natelson 1954
	0.6–1.2				Bellrose 1941
	<1.2		mixosaline	mud, clay	Harrison 1962
<1.2					Prophet and Carrillo 1979
1.2		little			Anderson 1950
1.2		little	mixosaline		Krapu and Duebbert 1974
<1.22		little	fresh		Jessen and Lound 1962
0.05–1.3			fresh		Van Donselarr et al. 1961
0.5–1.3				clay	Schwartz et al. 1986
≤1.4			mixosaline	clay, silt	Carter et al. 1985b
0.19–1.47	1.08–1.27	little	fresh	clay, clay loam	Jarvis et al. 1985
0.6–1.5					Walker 1965
0.9–1.5				clay	Brumsted and Hewitt 1952
1.2–1.5				organic	Tebo 1955
<1.5		moderate		silt, clay	Bergman 1973
<1.5	0.5–0.75		mixosaline	silt-sand	Verhoeven 1975
<1.5					Vander Zouwen 1982
≤1.5				silt	Jessen and Kuehn 1960
1.5					Smith 1946
1.5					Noyes 1983
0.05–1.6	0.65–0.8		mixosaline		Lindner 1978
1.25–1.65		little	mixosaline	silt	Schiemer and Prosser 1976
0.6–1.8				mud, sand	Sigler 1948
1.8			mixosaline	sand, mud	Thorne-Miller et al. 1983
1.1–1.9	1.6			marl	Bailey and Titman 1984
0.5–2.0		moderate	fresh	mud	Ho 1979
0.6–2.0	0.8–1.0	moderate	mixosaline		Davis and Carey 1981
<0.9–2.0			mixosaline	organic mud, clay	Lundegardh-Ericson 1972
1.0–2.0			mixosaline	sand-mud	Getsinger et al. 1982
	2.0		mixosaline		Ramirez and San Martin 1984
<2.0					Craig et al. 1980
0.44–2.06					U.S. Bureau of Reclamation 1986, unpublished
	<2.0		fresh	silt	McCombie and Wile 1971
<2.1	0.6–0.9				Telford and Stevens 1942
0.3–2.1	0.4–1.5		mixosaline	silt	Paullin 1973
1.2–2.28		moderate	mixosaline	mud	Mason and Bryant 1975
0.4–2.3			fresh	silt, clay	Gladyshev and Kogan 1977
≤2.4				muck, sand	Thomson 1944
<1.0–<2.5	<1.0	little	mixosaline	sand	Anderson and Jones 1976
0.5–2.5			mixosaline		Haslam et al. 1975
0.6–2.5				sand, mud	Spence 1964
1.4–2.5			mixosaline	sand-gravel	Downing 1975
<2.5	<0.7				Ozimek et al. 1986
<2.5	<1.0			sand, silt	Wilson 1941
1.5–2.7				organic	Kaul and Zutshi 1967
<1.0–<3.0	<1.0	moderate	fresh	silt, sand	Oglesby et al. 1976
0.2–3.0			mixosaline	sand	Verhoeven 1980a

Table 4. *Continued.*

Depth (m)		Water turbidity	Water salinity	Predominant substrate texture	Reference
Range or single observation	Optimum[a]				
0.3–3.0					Pammel 1917
	0.8–3.0		mixosaline		Howard-Williams and Liptrot 1980
<1.0–3.0	<1.0	little			Sheldon and Boylen 1977
1.0–3.0			mixosaline	sand	Howard-Williams and Davies 1979
1.0–3.0					Pirnie 1935
<3.0			fresh		Jenkin 1936
<3.0					Clayton and Bagyaraj 1984
<3.0			mixosaline	sand	Robarts and Allanson 1977
≤3.0		little		silt	Singhal and Singh 1978
3.0		little		silt	Stuckey 1971
3.0					Weisser and Howard-Williams 1982
>3.0		little	mixosaline	sand	Hill et al. 1975
0.8–3.35	0.0–1.0				Rickett 1922
1.25–3.5	1.25				Haag 1983
2.74–3.66					Evermann 1902
<3.7	1.8–3.0			muck	Moore 1915
3.0–4.0			mixosaline		Ravanko 1972
0.3–4.5		moderate		mud, sand	Denniston 1921
4.6					Modlin 1970
0.4–4.7	1.3–3.0		mixosaline	sandy mud	Kornas et al. 1960
<5.0	1.5–2.0	moderate			Seidelin Raunkiaer and Boye Petersen 1917
<5.0					Spence et al. 1979b
<5.0	<4.0				Voge 1987
<1.0–5.3					Denny 1973
0.5–5.5					Schmid 1965
0.0–6.0	0.75–1.5			clay, silt	Denny 1972
0.5–6.0	0.5–1.5	moderate		silty clay	Purohit 1981
0.8–6.2	1.5				Jerling and Lindhe 1977
<7.0	5.0–6.0	little	fresh		Seidelin Raunkiaer and Boye Petersen 1917
<1.0–7.0	<1.0		fresh	sand	Rickett 1922
<1.5–7.0				gravel, sand	Crum and Bachmann 1973
<1.5–7.0	1.5–2.0				Christensen and Andersen 1958
1.0–7.0		little		sand	Boltt et al. 1969
3.0–7.0	5.0	little			Sheldon 1987
4.0–7.0		little	fresh	gravel, mud	Singh 1981
<7.5			fresh		Golubic 1961
0.0–8.0	0.0–3.0		mixosaline		Kautsky 1987
<8.0	1.0–2.0			sand, mud	Olsen 1945
<8.0		little	mixosaline		Hammer and Heseltine 1988
<1.0–8.0	1.0–3.0	little	fresh	mud-marl	Rickett 1924
1.5–10.0					Jimbo et al. 1955
8.0–10.0			mixosaline		Wallentinus 1979

[a] Optimum depths as stated by author, where maximum biomass or frequency was shown in tables or graphs, or where best propagation results were obtained.

The U.S. Bureau of Reclamation (Garrison Diversion Unit Refuge Monitoring Annual Report 1989, unpublished) has 6 years of measurements on major environmental factors believed to affect sago production in a river in North Dakota and South Dakota. Their data suggest that annual water levels likely have little effect on turbidity, total dissolved solids (TDS), and nutrient loadings in the water column. Rather, poor sago production during years of high water levels seemed to be associated with a combination of depth and turbidity—which decreased photosynthesis—and lower water temperatures. These factors may have delayed sago growth during a critical late-May to mid-June period when plants must reach the surface and spread out horizontally to avoid competition for light from phytoplankton.

Ongoing experiments by Butler and Hanson (1985, 1986, 1988, unpublished) in a shallow freshwater Minnesota lake suggest that increases in depth combined with invasions of bottom-feeding rough fish can initiate a complex series of events that lead to increased turbidity and a permanent reduction of sago and other submersed macrophytes. After these events have occurred, they postulate that (1) greater water depth and increased bottom feeding combine to create an unfavorable light climate for submersed plants; (2) reduced plant biomass exposes more bottom sediments to wave energy and further reduces probability of winterkill; (3) reduced winterkill enlarges the fish community to include planktivorous species capable of overgrazing the zooplankton; (4) reduced zooplankton and increased nutrients caused by lessened macrophyte biomass increases phytoplankton; and (5) increased phytoplankton elevates summer pH and produces greater calcite precipitation which further increases turbidity.

To summarize, the depth distribution of sago is largely controlled by turbidity and wave action, but turbidity can be caused by a multitude of factors, many of which are poorly understood. Depth increases of only 40 cm can greatly reduce sago densities where light is limited by fine suspended silts or phytoplankton, and depth increases of only 10 cm can markedly reduce production where substrates are high in easily suspendible clays.

Transparency

Turbidity caused by particulate matter and plankton combines with color from physical and biological sources to decrease transparency of natural waters (Juday and Birge 1933). Water itself and the agents that cause turbidity also selectively absorb wavelengths important for plant photosynthesis (Wetzel et al. 1982).

Light attenuation and wave action usually control the maximum depth of colonization and zonation of submersed macrophytes (Boltt et al. 1969; Spence and Chrystal 1970; Schiemer and Prosser 1976; Spence 1982), although chance occurrence sometimes explains the variety of species found at any given depth (Denny 1973). Light quantity (photosynthetically active radiation or PAR), along with temperature, are the principal factors governing photosynthesis and growth in some submersed macrophytes (Wetzel and Neckles 1986). It was accepted for years that rooted vascular plants would grow to depths where irradiance of bottoms was only 1–4% of that striking the surface (Sculthorpe 1967; Hutchinson 1975). However, recent work by Chambers and Kalff (1985) indicated that angiosperm colonization ceases at depths where, on the average, 21% of PAR incident on the water surface is received during the growing season. However, older established plants may survive under lesser PAR values.

Sago growth can be greatly reduced by light attenuation caused by both organic and largely inorganic materials. Sago often grows in environments where wind action often suspends inorganic materials in the water column for variable periods. Such particles increase turbidity and reduce light needed for photosynthesis, but greatest production, especially of turions, often occurs on substrates composed of easily suspendible materials (Jensen 1940; Low and Bellrose 1944; Craner 1964; Sincock 1965; Smeins 1967). Growth of all submerged plants at such sites is usually limited to relatively shallow (<1.7 m) waters (Chamberlain 1948; Sincock 1965). Decreased water levels can more than overcome the effects of turbidity. Thus Bailey and Titman (1984) recorded a nearly 200% increase in sago biomass following a 17-cm decrease in water levels, even though turbidity slightly increased. Nonetheless, increased turbidity is the likeliest main reason why sago has disappeared from many wetlands (Bellrose et al. 1979).

Agricultural, domestic, and industrial pollution are well known sources of turbidity. Blooms of phytoplankton also are a major factor in the depth distribution of submerged macrophytes (Denniston 1921). Phytoplankton blooms limited sago to depths of 0.35–<1.5 m in the studies of Crum and Bachman

(1973), Andersen (1976), and Jupp and Spence (1977a). An often overlooked result of such blooms is the restriction of submersed macrophytes to shallowest nearshore areas where significant reductions in biomass caused by waterfowl grazing and wave action can occur (Jupp and Spence 1977a,b; Peterka and Hanson 1978).

Reduced radiation through screening by epiphytes in eutrophic waters has been blamed for the reduction of sago (Schiemer and Prosser 1976), as has shading by early-sprouting species of higher plants (Gorman 1979). Martin and Uhler (1939) stated that filamentous algae can nearly exclude sunlight and greatly reduce sago production in calm water areas. Recent theory (Phillips et al. 1978) suggests that in nutrient-rich waters, epiphytes and filamentous algae first blanket and shade out the submersed macrophytes; then phytoplankton blooms following decomposition as nutrients are released.

Colorimetric turbidity is negatively associated with sago production (Robel 1961b). It has been claimed that sago will grow to depths where light is 2.5–5.0% of that striking the water surface (Bourn 1932; Jensen 1940; Howard-Williams and Liptrot 1980), but these estimates are probably low (Chambers and Kalff 1985). Bourn (1932) lowered solar energy in greenhouse tanks from 12% to 9.5% of that outside the greenhouse by increasing water depth 0.6 m; this resulted in a 45% decrease in sago biomass. Kulberg (1974) found that in streams sago is absent at turbidities >153 Jackson Turbidity Units (JTU's). Otto and Enger (1960) showed that 100 ppm suspended sediments causes a 50% reduction in sago production in vessel tests. Sago was absent in parts of a New Zealand lake where suspended solids reached 100–300 mg/L, but was present in sheltered areas in water <1 m deep where 1–7% surface light occurred at 0.6 m (Gerbeaux and Ward 1986).

The data of Westlake (1967) was used by Kemp et al. (1981) to estimate the light compensation point for sago at 60 μE/m^2/s; this value, compared with that of common associates such as *Myriophyllum spicatum* and *Ceratophyllum demersum*, suggested that sago photosynthesizes at relatively low rates. This is true even under light saturation, and as light intensity decreases, net production of sago ceases at relatively high light levels. Thus, sago could be at a competitive disadvantage in turbid waters. Experiments of Madsen (1986) with Wisconsin plants also showed that photosynthesis in sago is rapidly light-saturated and that its net photosynthetic rate rises slowly with increases in temperature across the range 10–35°C. He achieved maximum net photosynthesis of 1.39 mg C/g ash-free dry weight per hour at 28°C when plants were subjected to 2,000 μE/m^2/s of PAR. Under controlled conditions, Hodgson and Otto (1963) observed that sago plants increased in weight but decreased in length at greater light intensities.

Symptoms of moderately reduced light intensity on sago include fewer and coarser leaves and stems and a lighter green color. Severe light reductions result in etiolation, lengthened internodes, stiffened leaves and stems, loss of branching, basal decay, and a tendency of leaves to protrude and wilt at the water surface (Bourn 1932). Anderson (1950) noticed that reduced light intensity increases the reproductive period of sago. Experiments of Van Wijk et al. (1988) showed that sago has adaptations to unfavorable light climates common to eutrophic or brackish waters. These adaptations likely differ among sago ecotypes and include increased relative turion production and increased shoot length. Plants can thus reach the water surface in an earlier stage and concentrate foliage in the surface layer.

Stuckey (1971) considered sago to have a wide tolerance to turbidity compared with other submersed macrophytes. This contention is supported by the surveys of Barker and Larson (1976), who found sago the only submersed hydrophyte in a muddy North Dakota river, but it was limited to calm sections where the sediment load was lessened. Reed (1979) found sago to be the only plant growing in murky water over chalky mud in a North Carolina estuary, and Bue (1956) observed sago to be the only submersed plant in a highly turbid South Dakota livestock pond overpopulated with fish. Reese and Lubinski (1983) found sago and *Potamogeton nodosus* the only remaining submersed macrophytes in the turbid lower reaches of the Ilinois River. Davis and Carey (1981) recorded a 157% increase in sago after storm damage and turbidity increases reduced total plant biomass 42% in Currituck Sound, North Carolina. A high tolerance of sago to shade is also indicated because the plant will grow under overhanging trees (Hynes 1970) as well as in the understory of emergent plants (Wilson 1958).

Haslam (1978) believed sago was intermediate in turbidity tolerance when compared with other submersed plants. This may be true under competition in grazed sites because sago grows new shoots from belowground rhizomes, whereas other species can grow new stems apically below clipped points (Cragg et al. 1980; Cohen et al. 1986).

In a polluted Egyptian lake, sago was absent where phytoplankton blooms reduced Secchi transparencies to 11–40 cm, but nearby, sago was abundant in water transparent to 60 cm (Aleem and Samaan 1969a). Similar results were reported by Gibbs (1973), who saw sago begin to recover in abundance in a New Zealand lake when Secchi disk readings exceeded 20 cm as a phytoplankton bloom diminished. Mason and Bryant (1975) found that sago was abundant in wetlands with Secchi transparencies as low as 66 cm, and the species was one of the major dominants in another water body where Secchi transparency was 60 cm (Engel 1984). Algal blooms that reduce light penetration to 10 cm can kill sago, but plants can grow well where Secchi transparency during the latter half of the growing season is 20–30 cm (Peterka and Hanson 1978). In an ongoing study, sago occurred in waters with Secchi disk readings as low as 33 cm (U.S. Bureau of Reclamation, Garrison Diversion Unit Refuge Monitoring Annual Report 1986, unpublished). Sago was absent where turbidity was >11.8 Nephelometric Turbidity Units (NTU's). Secchi and NTU values were negatively and positively correlated, respectively, with chlorophyll a, suspended inorganic matter, and suspended organic matter. Sago and other submersed vascular plants were absent from other lakes where Secchi disk readings were <20 cm because of algal blooms, but sago was abundant in a nearby lake where the Secchi transparency was 60 cm (Jenkin 1936). Rich (1966) found relatively low sago production and an almost total lack of turions in silty, carp-infested waters 45.7 cm deep where Secchi depths were <30 cm.

Sago beds increase water transparency by reducing water movement (Kollman and Wali 1976; Schiemer and Prosser 1976) and by oxygenating the water column; thus, they can contribute greatly to maintaining water quality, especially in wetlands where much of the bottom substrate is anaerobic (Stewart and Davies 1986). Increased transparency also is frequently observed in shallow or protected sites where sago helps anchor the substrate (Jackson and Starrett 1959). Increases in water transparency are often associated with other drastic changes in the environment. Steffeck et al. (1985) saw sago and many other hydrophytes increase in coverage during a dry year, when sediment contributions to the Mississippi River were presumably reduced. Water level fluctuations during the growing season decreased from an average of 3.2 m during the 4 years previous to the study, to 0.3 m during the year of the study, and water clarity increased—from 21–40 cm Secchi during the 2 years previous to the year when sago increased to 80 cm during the year the increase occurred. In a large shallow lake with a nearly flat clay bottom, I observed dense beds of sago and associated filamentous algae to nearly eliminate water turbidity by late July, except in a central area of greatest fetch where water depths were a few centimeters shallower. I attributed the slight reduction in depth of the sago-free central area to the great swelling properties of the fine clays deposited there (Kantrud 1986c, unpublished).

Observations by Whitfield (1986) emphasized the difficulty of separating the effects of changes in water transparency on sago growth from simultaneous changes in water level fluctuations, salinity, algal growth, and supplies of Ca in the water column. The precipitation of calcite by both biogenic and physical means cause lake "whitings" that can greatly increase turbidity (Strong and Eadie 1978; Weidemann et al. 1985). Preliminary work of Butler and Hanson (1985, 1986, 1988, unpublished) indicated that shallow (<1.5 m) freshwater wetlands having high proportions of Mg, Ca, and HCO_3 in the water column, adequate nutrients, long fetches, and rough fish populations are prone to high growing-season turbidities. A similar effect might result from suspended calcite crystals and phytoplankton, which allow sago growth only at very shallow depths. They postulated that, at low conductivities, small, colloidal-size calcite particles tend to repel each other and do not flocculate and settle. In turn, such small particles are easily suspended by rough fish and waves, an activity which adds to turbidity caused by phytoplankton. They further proposed that the dense phytoplankton populations are the result of reduced zooplankton grazers caused by an overabundance of planktivorous fish. In their studies, buckets of growing sago suspended 2 m deep in waters of 30-cm Secchi transparency received only 1.3% of surface irradiance and produced 4% the biomass of plants grown in buckets 0.5 m below the surface. Plants at the shallowest bucket depth received 25.7% of the incident light and were the only plants that produced drupelets.

In summary, the decreased transparency of waters inhabited by sago is caused by many common natural and man-made factors such as suspended organic and inorganic particles and phytoplankton. Sago biomass is also commonly reduced by shading or screening effects of filamentous algae or epiphytes. Sago photosynthetic rate is low and photo-

synthesis ceases at relatively high light levels, but the plant has important adaptations (some possibly genetically influenced) that allow it to succeed in highly turbid waters unfavorable to several common potential competitors. Nevertheless, Secchi transparencies less than 0.2 m usually indicate waters that will not support sago. According to the formula of Chambers and Kalff (1985), maximum depth for any angiosperm colonization under these conditions is 0.47 m. Sago beds can help increase water transparency by reducing water movement, providing a substrate for the growth of filamentous algae, and anchoring the bottom substrate. Recent research suggests that, at least in fresh waters, sago biomass can be limited by reduced water transparency caused by complex interactions among fish, invertebrate and phytoplankton populations, and water chemistry.

Chemistry

St. John (1916) described sago habitat as brackish, alkaline, or sometimes fresh waters. Seddon (1972) considered sago intolerant of conductivity below 200 μS and suspected higher nutrient requirements limited the plant's distribution. Recent work by Pip (1987)—who sampled for 17 *Potamogeton* species at 430 sites scattered across a large area of central North America—showed that waters inhabited by sago and *P. vaginatus* were significantly higher in TDS than for 14 other species. Mean TDS concentrations of the waters inhabited by sago, *P. vaginatus*, and *P. filiformis* were highest among the *Potamogetons*. These three are the only members of the linear-leaved subgenus *Coleogeton* (at least in North America), which suggests that the linear-leaved growth form is an adaptation to increased salinity.

Optimum salinity for sago in thalassic waters is 5–14 g/L (Sincock 1965; Orth et al. 1979; Verhoeven 1980a), and the species is generally replaced by algal or *Ruppia*-dominated communities at 13–20 g/L in coastal areas (Verhoeven and Van Vierssen 1978a,b; Spence et al. 1979b). Optimum salinity in athalassic Cl- and SO_4-dominated waters is 3–6 g/L and 2–15 g/L, respectively (Jensen 1940; Stewart and Kantrud 1972; Millar 1976). In North Dakota wetlands, sago is usually replaced by *Ruppia* in SO_4-dominated waters at salinities more than 26 g/L and in HCO_3-dominated waters by many types of other submersed macrophytes at salinities less than 0.7 g/L (Stewart and Kantrud 1972). However, Hammer and Heseltine (1988) found sago and *Ruppia* coexisting in waters of 53 g/L salinity in SO_4-dominated lakes in the Canadian prairies. They suggested that sago does not flower in waters where salinity exceeds 45 g/L.

Measurements of salinity or electrical conductivity are often used to place approximate upper limits on the tolerance of sago for highly mineralized waters. Worldwide, sago grows—or at least its propagules survive—in natural waters with salinities up to 104 g/L TDS (Table 5). At the other extreme, sago has been recorded in natural waters with as little as 35 mg/L TDS (Pip 1987). In addition, sago is readily cultured in distilled water (Bourn and Jenkins 1928; Huebert and Gorham 1983). Upper limits for this species seem to vary greatly in soils or waters dominated by different anions, but this relation remains unproven. Hammer and Heseltine (1988) found no ionic effects on sago in prairie lakes of Canada dominated by various anions and cations. Nevertheless, sago seemingly survives 18–21 g/L TDS in Cl-dominated thalassic areas (Olsen 1950; Mathiesen and Nielsen 1956; Spence et al. 1979b; den Hartog 1981; Van Vierssen and Verhoeven 1983); 50 g/L TDS in inland areas rich in CO_3 or HCO_3 (McCarraher 1977); and 104 g/L in inland waters extremely high in SO_4 (Ungar 1970).

Pip (1984) showed that sago maintains its affinity for waters high in TDS between regions of different

Table 5. *Salinities of sago-inhabited waters, arranged according to increasing maximum observed salt tolerance.*

Salinity or total dissolved solids (mg/L)[a]			
Range or single observation	Optimum	Dominant cations	Reference
50–70			Sheffer and Robinson 1939
91			Fraser and Morton 1983
127–141			Crowder et al. 1977
>140			Seddon 1972
<175			Gorman 1979

Table 5. *Continued.*

Salinity or total dissolved solids (mg/L)[a]			
Range or single observation	Optimum	Dominant cations	Reference
210		CO_3	Jenkin 1936
	>210		McCombie and Wile 1971
158–245			Carter et al. 1985b
98–248			Kowalczewski 1975
189–267			Ozimek 1978
>105–>260			Merry et al. 1981
192–262			Engel 1984
180–300			Singh 1981
140–350			Vass 1980
<350			Lohammar 1965
458			Disrud 1968
454		SO_4	Gladyshev and Kogan 1977
280–490			Downing 1975
353–546		CO_3	Gibbs 1973
490			Ellis 1955
>800			Chapman 1960b
910			Madsen et al. 1988
1,097		SO_4	Olson 1979
1,260		HCO_3/SO_4	Schiemer and Prosser 1976
140–1,300			Smith 1973
1,670		Cl	Harrison 1962
840–1,899		Cl	Craner 1964
2,200			Dix and Smeins 1967
144–2,573		Cl	Spence et al. 1979a
3,000			Fletcher et al. 1985
748–3,114		Cl	Congdon and McComb 1976
3,160			Anderson and Jones 1976
<320–3,195		Cl	Chapman 1960a
1,050–4,000		CO_3/HCO_3	Paullin 1973
>4,000		CO_3/HCO_3	Reynolds and Reynolds 1975
3,120–4,070		Cl	Zaky 1960
4,300–4,500		Cl	Lundegardh-Ericson 1972
<5,000		Cl	Haslam et al. 1975
2,000–5,000		Cl	Getsinger et al. 1982
3,000–5,000		Cl	Ungar et al. 1969
24–5,533			Pip 1984, 1987
612–5,567	4,567		Barker and Fulton 1979
∿5,800		Cl	Evans 1953
2,800–5,900		Cl	Katanskaya 1986
	3,000–6,000	Cl	Jensen 1940
5,000–6,000		Cl	Ravanko 1972
∿6,500		Cl	Kautsky 1987
1,980–6,870		Cl	Bourn and Jenkins 1928
1,000–7,000		Cl	Brock and Lane 1983
<7,000		Cl	Neely 1962
6,000–7,000		Cl	Kornas et al. 1960
7,000		Cl	Barnes et al. 1971
	4,700–7,050	Cl	Verhoeven 1975
35–7,900		SO_4	Pip 1979
8,000		Cl	Hill et al. 1975
<8,500		Cl	Ward 1976

Table 5. *Continued.*

Salinity or total dissolved solids (mg/L)[a]			
Range or single observation	Optimum	Dominant cations	Reference
2,000–9,000		Cl	Robarts and Allanson 1977
	9,000	SO_4	Shubert 1982
9,000		Cl	Oborn 1964
<9,500		Cl	Kiorboe 1980
<10,000		Cl	Massart 1922
<10,000		Cl	Howard-Williams and Liptrot 1980
<10,000		Cl	Klokov and Zimbalevskaya 1974
1,400–10,700		Cl	Southwick and Pine 1975
<11,000		Cl	Carter et al. 1985a
5,000–11,000		Cl	Howard-Williams and Davies 1979
1,030–11,680		Cl	Flowers 1934
1,000–12,000		CO_3/HCO_3	McCarraher et al. 1961
4,000–12,000		Cl	Stewart and Davies 1986
5,500–12,000		SO_4/Cl	Krapu and Duebbert 1974
10,000–12,000		Cl	Klavestad 1957
12,000	7,000	Cl	Bourn 1932
12,000			Academia Sinica 1979, cited in Hammer and Heseltine 1988
≥12,000	7,000	Cl	Critcher 1949
13,000		Cl	Martin and Uhler 1939
2,530–13,010		Cl	Verhoeven and Van Vierssen 1978a
	7,000–14,000	Cl	Sincock 1965
7,500–14,000		Cl	Olsen 1945
<14,460		Cl	Verhoeven and Van Vierssen 1978a
	1,000–15,000	SO_4	Sloan 1970
4,000–15,000		Cl	Thorne-Miller et al. 1983
97–15,130			Kadono 1982
~16,000		Cl	McAtee 1939
<16,260	<5,420	Cl	Verhoeven 1980a
10,850–16,550		SO_4	Huntsman 1922
200–18,000		Cl	Olsen 1950
<18,000		Cl	Mathiesen and Nielsen 1956
18,000		Cl	den Hartog 1981
6,000–19,000			Drabkova et al. 1978, cited in Hammer and Heseltine 1988
5,000–20,000		Cl	Gerbeaux and Ward 1986
20,000		Cl	Spence et al. 1979b
200–20,380		SO_4	Rawson and Moore 1944
3,265–20,961	5,421–12,649	Cl	Van Vierssen and Verhoeven 1983
2,400–22,400	3,300–7,200	Cl	Wright et al. 1949
1,000–24,000			Smeins 1967
3,300–25,000		SO_4	Hammer et al. 1975
225–26,400	2,000–15,000	SO_4	Stewart and Kantrud 1972
0–31,500	2,000–15,000	SO_4	Millar 1976
131–32,637			Sletten and Larson 1984
350–35,873		SO_4	Metcalf 1931
<49,918		CO_3/HCO_3	McCarraher 1977
<53,000		SO_4	Hammer and Heseltine 1988
2,300–104,000		SO_4	Ungar 1970

[a]Conductivity was converted to mg/L with the following multipliers: 0–2 mS × 0.7; 2–40 mS × 1.0; >40 mS × 1.5. Chlorinity (0/00) was converted to mg/L by multiplying by 1.807 × 10 3; sea strength was considered 31,950 mg/L.

geologic origin. Table 1 shows 19 optimum growth depths for sago in mixosaline waters, but only 3 for fresh waters. Downing (1975) opined that sago could not compete with submersed macrophytes in waters with only 280–490 mg/L TDS except in exposed sites. In the more arid regions of interior North America, sago grows in a regime of increasing water salinity during the growing season (Craner 1964; H. A. Kantrud, unpublished data).

Teeter (1963, 1965) conducted extensive culture experiments to determine the effects of NaCl salinity on the growth and reproduction of sago. He found that concentrations of 3 g/L stimulate but more than about 6 g/L curtail turion growth, and that vegetative production decreases and drupelet germination time increases at salinities greater than 3 g/L. Outdoor tank experiments of Lumsden et al. (1963) with thalassic waters indicated that drupelets are not produced at salinities greater than 3.8 g/L and that turion production increases uniformly as salinities increase from 0.6 to 5.4 g/L.

Van Wijk et al. (1988) cultured sago indoors, using plants taken from waters that varied from fresh to brackish (oligohaline to mesohaline) and grew the cultures in water varying from fresh to 9 ppt Cl^- (16 g/L). Plants from freshwater habitats produced many double turions while plants from brackish habitats only rarely produced double turions. Plants from freshwater populations produced turions in an earlier stage of growth, compared with plants from brackish habitats. Plants from brackish-water populations usually had more shoots and biomass production when grown at 3 ppt Cl^- (5.4 g/L), whereas plants from freshwater populations grew best in fresh water. Shoot length and biomass decreased considerably at 9 ppt Cl^- in all populations.

In general, optimum shoot numbers and biomasses occurred at salinities coinciding with those found in the natural habitats for each population. The way in which sago adapts to salinity, and the actual salt-tolerating mechanism involved, remains unclear. The experiments of Van Wijk et al. (1988) also indicated genetic differentiation and the existence of ecotypes.

Field studies in NaCl-dominated waters revealed negative correlations between salinities >1.9 g/L and both vegetative growth and production of drupelet heads (Craner 1964). Sago grown from turions in distilled water does not produce inflorescences (Huebert and Gorham 1983). Results of several of the earlier culture experiments mentioned in this section were summarized by Christiansen and Low (1970).

Sago seems little affected by relatively slow salinity fluctuations within the species' range of tolerance. Thus sago persisted in an estuarine system where annual fluctuations of up to 14 g/L occurred (Howard-Williams 1978), and it survived in an inland, SO_4-dominated wetland where salinity increased 81 g/L between growing seasons (Ungar 1970).

A regular cycle of sago growth and decline occurs in Lake Ichkeul, Tunisia, where salinities of 40 g/L occur by the end of summer as the sea flows in. Winter rains then freshen the lake for spring growth of sago and other hydrophytes (Skinner and Smart 1984). There is also evidence that sago can increase in estuaries after major storms lower salinities (Kerwin et al. 1976). Sago often shows great variation in annual abundance in many wetlands in the climatically unstable prairie region of North America where salinities are raised by evaporation and lowered by precipitation (H. A. Kantrud, personal observation).

Iversen (1929) considered sago characteristic of persistently alkaline waters (pH 7.0–9.0). Wiegleb (1978) recorded sago in seven of nine wetlands with maximum pH>9.0. Mean pH of 116 sites inhabited by sago throughout a large area of central North America was 8.5; significantly higher pH was measured where the species was present than where it was absent (Pip 1987). She also showed that, with respect to pH, sago had a greater number of significant differences with other *Potamogetons* than all but the acidophilic *P. epihydrus*, and that the mean pH of sago-inhabited waters was higher than for waters inhabited by all the other 16 *Potamogetons* studied except *P. friesii*.

Although sago will flourish in bottom substrates with pH as low as 4.6 (Denny 1972), the species has an aversion to acidic waters (Jeglum 1971; Merry et al. 1981; Kadono 1982; Pip 1984). Sago was lost from the flora of a reservoir when pH fell below neutrality (Hinneri 1976). Although sago has not been recorded in waters with pH<6.3, it will photosynthesize at pH>10.5 and has been recorded in waters up to pH 10.7 (Table 6). Penuelas and Sabater (1987) showed that sago abundance was negatively correlated with pH along the course of a river.

Luxuriant growth of submersed macrophytes can be accompanied by increases in water column pH as plants take up CO_2 and HCO_3. However, when pH

Table 6. *Chemical content of natural waters inhabited by sago pondweed.*

Characteristic	Unit of measure	Range or single observation (reference[a])
pH and alkalinity system		
pH		6.3–10.7 (1;2)
Total alkalinity	g/L $CaCO_3$	0.018–34.7 (3;4)
HCO_3 alkalinity	g/L $CaCO_3$	0–20.2 (4)
CO_3 alkalinity	g/L $CaCO_3$	0–25.4 (4)
CO_2	mg/L	0–9 (2)
Total hardness	g/L $CaCO_3$	0–14.0[b] (4;5)
Noncarbonate hardness	mg/L $CaCO_3$	57–3,700 (6)
Nutrient system		
NO_3–N	mg/L	0–22.7 (7;8)
NO_2–N	mg/L	0–0.32 (9;10)
NH_3–N	mg/L	0.01–10.6 (11;12)
Organic-N	mg/L	<8.74 (13)
SRP	mg/L	0–44 (14)
SUP	µg/L	1–10 (15)
Total P	mg/L	<646 (15)
K	mg/L	0.8–270 (9;6)
Other ions and compounds		
Al	mg/L	0–48.0 (16;9)
As	µg/L	9–200 (6)
B	mg/L	0.57–2.9 (6)
Ba	µg/L	100–200 (6)
Ca	mg/L	0–565 (4)
Cd	µg/L	0–4.15 (6;18)
Cl	mg/L	0–10,517 (14;19)
Co	µg/L	0–2 (6)
Cr	µg/L	0–30 (6)
Cu	µg/L	0–180 (6;17)
Fe	mg/L	0–1.0 (13)
Fl	µg/L	100 (6)
Hg	µg/L	0.1–0.5 (6)
Li	mg/L	0.46–1.8 (6)
Mg	mg/L	0–3,400 (4;5)
Mn	µg/L	10–150 (13)
Mo	µg/L	3–16 (6)
Na	mg/L	2.6–5,890 (9;20)
Ni	µg/L	3–170 (6;17)
O_2	mg/L	4.6–22.2 (21;22)
Pb	µg/L	3–10 (6)
S	mg/L	0.2–4.4 (5)
Se	µg/L	1 (6)
SiO_2	mg/L	0.08–69 (4)
SO_4	mg/L	0–10,000[b] (14;6)
Sr	µg/L	410–970 (6)
Va	µg/L	4–14 (6)
Zn	µg/L	4–140 (6;17)
Chlorophyll *a*	µg/L	0.01–11.98 (23;24)

[a]Reference: (1) Moyle 1945; (2) Hellquist 1975; (3) Spence et al. 1979a; (4) McCarraher 1977; (5) U.S. Army Corps of Engineers 1984, unpublished data, West Stump Lake, North Dakota; (6) U.S. Geological Survey 1976 to 1979, unpublished data. West Stump Lake, North Dakota; (7) Olson 1979; (8) Holmes and Whitton 1977; (9) Harris and Silvey 1948; (10) Ho 1979; (11) Gibbs 1973; (12) Kulshreshtha and Gopal 1982; (13) Krapu and Duebbert 1974; (14) Pip 1979; (15) Howard-Williams 1981; (16) Deevey 1957, cited in Cole 1963; (17) Kollman and Wali 1976; (18) Adams et al. 1980; (19) Spence et al. 1979a; (20) Hill et al. 1975; (21) Chapman 1960a; (22) Billore and Vyas 1981; (23) Jupp and Spence 1977a; (24) Vermaak et al. 1981.

[b] = low.

is raised by algal blooms, precipitation of fine particles of calcite in the water column may add to high turbidity and cause poor sago production (Butler and Hanson 1985, 1986, 1988, unpublished).

Sago stands alone among the *Potamogetons* in tolerance to alkalinity (Hellquist 1975). Of 68 Wisconsin lakes surveyed by Steenis (1932), sago was abundant only in the lake with highest (32.5 mg/L) $CaCO_3$ alkalinity. Moyle (1945) placed sago among a group of species that inhabited Minnesota waters with alkalinity always >15 mg HCO_3/L and that do best where minimum alkalinities are >30 mg HCO_3/L. Spence (1964) considered sago characteristic of lakes with $CaCO_3$ alkalinities >60 mg/L, and in later surveys Spence et al. (1979a) found no sago in Scottish lochs where total alkalinity was <17.7 mg/L. Hellquist (1980) placed sago with only two other species (*P. hillii* and *P. vaginatus*) in a group of plants characteristic of New England waters with HCO_3 alkalinity >109.8 mg/L. Kadono (1982) and Pip (1987) found significantly higher alkalinity in waters supporting sago than those that did not. Among 17 species of *Potamogeton*, the mean total $CaCO_3$ alkalinity for sago-inhabited sites (163 mg/L) was exceeded only by sites supporting *P. vaginatus* (179 mg/L; Pip 1987). Hellquist (1980) found the range of HCO_3 alkalinity in waters supporting sago (36.6–282.5 mg/L) to be exceeded only by that of *P. nodosus*. Penuelas and Sabater (1987) found sago abundance positively correlated with alkalinity along the course of a river. Sago was lost from the flora of a reservoir when HCO_3 reserves were replaced by free CO_2 (Hinneri 1976). Luxuriant sago growth consumes large amounts of CO_2 and can cause rapid decreases in total alkalinity of the water column (Aleem and Samaan 1969a).

Data of McCarraher (1977) show for the CO_3/HCO_3-dominated lakes of Nebraska that sago at least survived in Reno Lake (CO_3 alkalinity 25.4 g/L, total alkalinity 34.7 g/L) and Moffit Lake (HCO_3 alkalinity 20.2 g/L), and plants were collected in other lakes with 9.0 g/L total alkalinity. Dominant cations in these lakes were Na and K, and salinities were high (33–37 g/L TDS). These lakes were low in SO_4 and so do not support the hypothesis of Reynolds and Reynolds (1975) that sago and other euryhaline plant species can tolerate much higher alkalinities and salinities in wetlands where SO_4 rather than CO_3 or HCO_3 are the dominant anions. Reynolds and Reynolds (1975) did not find sago in CO_3/HCO_3 lakes in British Columbia where Na or Mg were the dominant cations and salinities were >24 g/L TDS.

Competition for the inorganic carbon associated with the alkalinity system may be one of the most important factors determining plant species composition in nutrient-rich fresh waters, especially if phytoplankton are involved (Maberly and Spence 1983). Kollman and Wali (1976) measured CO_3 and HCO_3 in a lake where sago was the monodominant submersed macrophyte and found that HCO_3 levels may limit the productivity of sago in alkaline waters where the plants must use this ion as a carbon source (see Physiology). Pip (1984) showed that sago-inhabited waters averaged higher in alkalinity in a region where levels were generally lower than in an area where levels averaged higher, postulating the reason to be more intense competition from the large number of specialist taxa that inhabit soft waters.

Culture experiments of Huebert and Gorham (1983) showed that sago cannot mobilize enough inorganic C from the bottom sediments and that plants need a minimum of 30.5 mg/L HCO_3 in the water phase to allow survival and normal growth. Sago can be found in lakes where HCO_3 cannot be detected during the growing season, but in these lakes CO_3 is present at ≥68 mg/L (McCarraher 1977). The U.S. Bureau of Reclamation (Garrison Diversion Unit Refuge Monitoring Annual Report, 1986, unpublished) found sago presence significantly related to greater and lesser amounts of CO_3 and HCO_3, respectively, which indicates uptake of HCO_3. Uptake of HCO_3 was also indicated in the studies of Purohit et al. (1986), who showed that harvest of sago plants increased concentrations of both free CO_2 and HCO_3 during months when peak sago biomass normally would occur.

Wiegleb (1978) differentiated the normal form of sago (var. *vulgaris*) from a very narrow-leaved form (var. *scoparius*) which grew in HCO_3-poor waters.

The relation of turbidity to alkalinity is unclear. Butler and Hanson (1985, 1986, 1988, unpublished) suggested that the negative correlation they found between total alkalinity and turbidity in a freshwater lake dominated by HCO_3 could indicate that turbidity is caused by colloidal particulates that act as binding sites for dissolved ions in the water column. They further postulated that, at the lake's low electrical conductivities, these particles repel one another and remain in suspension, rather than flocculating to a size that promotes settling. Even if extended calm weather allowed some of these particulates to settle, minimal sediment disturbance would quickly resuspend them, again raising turbidity. Perhaps the opposite situation occurs in the highly alkaline, mixosaline waters favored by sago

in prairie wetlands. There, calcite particles aggregate and fall to the bottom as spring water temperatures increase, clearing the water and allowing rapid growth of sago and benthic algae, which in turn help protect the bottom from disturbances by wave action.

Although the distribution and production of sago likely is seldom limited by water column nutrients (Peltier and Welch 1969), growth of the plant has often been associated with polluted, oxygen-poor wetlands high in nutrient ions. Of 10 dense stands of sago investigated by Prejs (1986b), 5 were affected by municipal wastes, whereas none of 12 sparse stands were. Efforts have been made to control sago in eutrophic streams where the plant can cause unacceptably low nighttime O_2 levels (Madsen et al. 1988).

Data in Appendix B suggest that sewage and agricultural effluents are more frequently associated with eutrophication of waters supporting sago than are domestic animal wastes and industrial effluents, but the two former sources of pollution probably are more common. Eutrophic, but not hypereutrophic, waters supported higher sago biomass in the lake surveys of Ozimek et al. (1986), who also found greater biomass and more rapid growth of the plant in polluted versus unpolluted sites in the same lake.

Growth of sago in nutrient-rich waters is frequently noted in the lower reaches of rivers and streams, where pollution loads are usually greatest. However, extremely high nutrient loadings can destroy or injure the plant and result in its replacement by algae (Pieczynska and Ozimek 1976; Howard-Williams 1981). In a group of polluted English wetlands that had suffered the loss of many macrophyte species, sago showed best survival in those with lowest input of agricultural fertilizer (Mason and Bryant 1975). As lake eutrophication proceeds, sago biomass decreases in shallower zones, and plants disappear from deeper zones where light intensities are lowest (Bumby 1977). In a turbid, highly eutrophic, carp-infested reservoir on the Minnesota–South Dakota border, small, unhealthy-appearing sago plants existed only at depths <8 cm (Kantrud 1984, unpublished).

Vigorous sago growth is often associated with decreased total N, NO_2, NO_3, or NH_3 levels in the water or bottom sediments during the growing season (Jensen 1940; Aleem and Samaan 1969a; Ho 1979; Shubert 1982). This indicates plant uptake. However, sometimes no relation is evident (Wong and Clark 1976; Purohit and Singh 1981). For example, in a polluted Wisconsin stream, Madsen (1986) found that the luxuriant sago community held only 5.2% of the daily loading of N into the system. Purohit (1981) found that total N in the water column positively correlated with sago biomass, but that NO_3–N negatively correlated; N in plant tissues seemed independent of total N in the water column.

Data in Table 6 show the wide ranges in various forms of N found in sago-inhabited waters. Concentrations of NO_3–N in the water column of a sago-dominated South African lake decreased 13% (from 1.69 mg/L to 1.47 mg/L), even though sago biomass increased 20 times during the 2 years (Vermaak et al. 1983). Concentrations of N in sago tissue can be 1.8×10^3–5.4×10^3 times that of the water column (Gopal and Kulshreshtha 1980). Even so, it is unlikely that sago growth is limited by inadequate N in the water column in most natural waters because of the plant's ability to mobilize this nutrient from bottom sediments (Peltier and Welch 1969; Huebert and Gorham 1983). The relation between N in sago and in the water column often is obscured by high N consumption by algae (Howard-Williams 1981) and inputs from plant decomposition and surface runoff (Hutchinson 1957; Paullin 1973).

Pip's (1987) survey of 430 *Potamogeton*-inhabited sites showed that waters supporting sago and the closely related *P. vaginatus* were significantly higher in combined NO_2 and NO_3–N than waters where the two species were not found. Mean N concentrations for the two species were 1.55 and 1.48 mg/L, respectively—the highest among the 17 species of *Potamogeton* studied. Earlier work (Pip 1984) showed that sago-inhabited waters averaged higher in these ions in a geographic region where levels were generally lower than in a region where levels averaged higher.

Several other investigations of lakes, streams, and reservoirs (Kaul and Zutshi 1967; Kaul 1977; Janauer 1981; Peverly 1985; U.S. Bureau of Reclamation 1986, unpublished; Penuelas and Sabater 1987) have related the presence or abundance of sago to higher levels of various N ions. Other studies (Fetter et al. 1978; Wiegleb 1978; Kohler and Zeltner 1981, cited in Haslam 1987) indicated that certain levels of these ions can be toxic to sago, particularly the NH_3 ion at levels >0.4 mg/L. Purohit et al. (1986) suggested that forms of N other than NO_3 can be

used by sago, and Wiegleb (1978) considered sago indifferent to NO_3 concentrations.

I conclude that, regardless of the forms of N most used or their sources in the environment, sago seems strongly associated with higher levels of this element. However, the plant has a great ability to absorb N and compete for it in aquatic ecosystems where concentrations of this important nutrient are low. Thus, the distribution and abundance of sago probably are seldom limited by the availability of N.

Phosphorus is widely regarded as the most important nutrient limiting primary productivity. Sago production is associated with high or elevated amounts of P in the water column (Zaky 1960; Jones and Cullimore 1973; Jupp and Spence 1977b; Anderson 1978; Pip 1978; Janauer 1981; Collins et al. 1987; Penuelas and Sabater 1987). Low or decreasing P concentrations during peak periods of sago growth have been recorded in waters of lakes and rivers (Jensen 1940; Aleem and Samaan 1969a; Paullin 1973; Kollman and Wali 1976; Ho 1979; Purohit 1981; Purohit et al. 1986). Changes in soluble reactive P (SRP) values in the water column can be difficult to detect or largely caused by nonbiological activity where values are low (<5 μg/L), even in dense sago stands (Howard-Williams and Allanson 1981).

Sago has been found in lakes with up to 646 mg/L P (Deevey 1957, cited in Cole 1963) and in waters where SRP could not be detected (Pip 1979; Table 6). Low levels likely indicate uptake, as growing sago, with its epiphytic algae, is a net accumulator of P from the water column (Howard-Williams and Allanson 1981; Vermaak et al. 1983) and does not leak the element as some common submersed plants are thought to do (Madsen 1986).

Sago uses roots and shoots to obtain P (Welsh and Denny 1979). Sediment P is usually not as readily available to sago as sediment N (Peltier and Welch 1969; Jones and Cullimore 1973; Huebert and Gorham 1983). However, sediments are the major source of P for sago, under aerobic conditions and where water-column SRP is low and is rapidly taken up by other organisms, including periphyton on sago leaf surfaces (Howard-Williams and Allanson 1981). Thus, under such circumstances, direct transfer of phosphates from sediments to the water column by sago is unimportant, leading Vermaak et al. (1983) to consider the plant a P reservoir instead of a pump.

Sago shoots can contain as little as 5 times or as much as 7,000 times the P found in the water col-umn (Gopal and Kulshreshtha 1980; Vermaak et al. 1983). However, P contained in leaf periphyton can easily confuse such measurements, and it is possible that this community may even assist in P absorption (Howard-Williams and Allanson 1981). Wong and Clark (1976) and Ho (1979) recorded good correlations between water column P and P concentrations in sago tissue. Pip (1987) found that sago differed from other species of *Potamogeton* with respect to P concentrations in the water column; she also found P concentrations in 116 sago-inhabited sites in North America ($\bar{x}$ = 3.83 mg/L, range 0–31.3 mg/L) significantly higher than at sites where sago was not present. Despite these results, water column P is not a significant factor in sago distribution over large geographic areas of North America (Hellquist 1975; Pip 1984).

The effects of P uptake by sago on the aquatic environment depend on the abundance and availability of the element. Purohit and Singh (1981) found no detectable differences in P between water sites where sago growth was dense or sparse. Madsen (1986) determined that, even at the peak of the growing season, a luxuriant sago-dominated community in a polluted Wisconsin stream held only 1.9% of the daily loading of P into the stream. Conversely, Purohit et al. (1986) estimated that, at the period of peak macrophyte biomass, a community of hydrophytes where sago was abundant contained 96% of the total P in the littoral system, excluding bottom substrate and other biota.

Jones and Cullimore (1973) and Getsinger et al. (1982) indicated that sago lacks the ability to compete with common associates such as *Ceratophyllum demersum* and *Potamogeton richardsonii* in aquatic systems low (perhaps <1.0 mg/L) in water column P. The only exception to this trend was in a lake dominated by *Myriophyllum spicatum*, where P was high in both water column and sediments.

Where sago is absent and P is abundant in the water column, other factors, especially turbidity, probably limit sago growth (Fetter et al. 1978), although in some instances lush sago growth can control P availability and suppress light-limiting phytoplankton blooms (Vermaak et al. 1981). When P was added to a community of sago and filamentous algae, the algae quickly absorbed most of the P, and increases in P content of sago were noticed only at high levels of enrichment (Howard-Williams 1981). Vermaak et al. (1983) postulated that P can be absent from the water column of a sago-

dominated lake high in $CaCO_3$ through precipitation of apatite ($Ca_5FP_3O_{12}$).

Studies of Jupp and Spence (1977a,b) and Van Vierssen and Verhoeven (1983) showed that phytoplankton blooms, sufficient to lower sago productivity, have occurred in wetlands in temperate climates where P concentrations ranged from 0.05–1.5 mg/L. Sago and other submersed macrophytes can be restricted to shallow (<1 m) waters under such conditions (Jupp and Spence 1977a,b). However, phytoplankton productivity was very low in a South African lake perennially dominated by sago where water column P was <0.2 mg/L (Vermaak et al. 1983). In this lake, much P was concentrated in the sediments, and benthic algae carpeted the bottom during the winter period of low sago biomass (Vermaak et al. 1983). Thus, the interactions of P, sago, and phytoplankton blooms differ with climate or perhaps other correlated factors.

I conclude that large amounts of water column P can be tolerated by sago and taken up by roots and shoots, but that the plant is poor at extracting the element from sediments. Sago is less competitive with other angiosperms in ecosystems low in P. The plant shows a greater affinity for waters high in P than other members of the genus but, in such waters, often suffers from turbidity caused by phytoplankton, especially at deeper sites. This could greatly restrict sago production in deeper waters of temperate climates where the plant is forced to regenerate from turions each spring. The effects of P may be associated with other aspects of water chemistry, and the element likely is easily lost from the water column.

Potassium is essential for sago growth (Devlin et al. 1972), but few studies of the effects of water column K on sago and its environment have been conducted. Sago has been recorded as most abundant in lakes and streams with higher amounts of this element in the water column or interstitial sediment water (Kaul and Zutshi 1967; Kaul 1977; Peverly 1985), but K does not seem to be limiting in natural waters. Madsen (1986) found that a luxuriant sago-dominated community held only 4.2% of the daily loading of K into a polluted Wisconsin stream, even during maximum plant biomass. Sago has been found in waters with an extreme range in K concentration (Table 6).

Culture experiments of Huebert and Gorham (1983) showed that when K is absent from the water column, Na replaces it, although plant vigor suffers.

Kollman and Wali (1976) found increases in K in both the water column and sediments during the growing season, which they thought were caused by evaporation and equilibrium shifts of the element from water to sediment. At the same time, K concentrations in sago rose rapidly through the growth period, declined during the reproductive period, and then increased at senescence. K levels in the water column decreased only slightly as the amount in sago rose rather abruptly during the peak growth period (Ho 1979).

Sago can tolerate at least 10 g/L of either Cl or SO_4, and also high levels of Na, Mg, and many other elements (Table 3). In some waters where Cl is the dominant cation, sago does best where Cl content is 2.6–5.0 g/L; below and above this level *Myriophyllum spicatum* and *Ruppia* spp., respectively, were the most abundant plants (Verhoeven 1975, 1980a). In other such waters, sago prospered where Cl was about 3–9 g/L and occurred as the only submersed macrophyte where summer concentrations were as high as 11.6 g/L (Van Vierssen and Verhoeven 1983). Here, *Ruppia* spp. were remarkably absent, even at higher Cl concentrations, and *Zannichellia palustris* and *Ranunculus baudotii* occurred where Cl levels were below 5 g/L.

Sago was the only one of 17 species of *Potamogeton* studied by Pip (1987) that showed significantly higher mean Cl levels ($\bar{x}$ = 70 mg/L, range 0–1,234 mg/L) and mean SO_4 concentrations ($\bar{x}$ = 76 mg/L, range 0–3,403 mg/L) in waters where sago was present. In addition, it was the only species significantly different from the others with respect to Cl or SO_4 concentrations. Kadono (1982) and the U.S. Bureau of Reclamation (Garrison Diversion Unit Refuge Monitoring Annual Report 1986, unpublished) also noted that Cl levels were higher in waters supporting sago. Penuelas and Sabater (1987) found that sago abundance was highly correlated with SO_4 concentrations along the course of a river.

Sincock (1965) thought that sago growth and turion production were enhanced in estuarine waters of 7–14 g/L salinity in which Ca, Mg, and K were found in approximately equal amounts. Lohammar (1938) and Hutchinson (1975) stated that sago has a high (≥25 mg/L) requirement for water phase Ca. Kaul and Zutshi (1967), Kaul (1977), and Kadono (1982) also noted that larger amounts of Ca were associated with larger amounts of sago, although Purohit and Singh (1981) found no detectable dif-

ferences in Ca concentration between sites in waters where sago growth was luxuriant or sparse. At least 2 ppm water phase Ca is required to partly or fully counteract the toxic effects of other ions present in the water phase (Huebert and Gorham 1983).

In rivers, sago can be restricted to lower reaches where waters are highest in Ca (Merry et al. 1981). In one instance, the inflow of Ca-poor river water into a lake where the plant occurred reduced Ca concentrations to limits lethal to sago (Allanson and Howard-Williams 1984; Whitfield 1986).

Sago, likely through a symbiont bacterium (Oborn 1964), precipitates calcite ($CaCO_3$) on leaves, stems, and in lacunae; this mineral encrustation can compose nearly 12% of plant dry weight (Oborn 1964). Thus Ca concentrations in the water column decrease during periods of rapid sago growth (Ho 1979), or cause the presence of sago to correlate with lower Ca values in the water column (U.S. Bureau of Reclamation Garrison Diversion Unit Refuge Monitoring Annual Report 1986, unpublished). However, this phenomenon may not be observed in wetlands subject to large losses of water through evaporation (Kollman and Wali 1976). McCarraher (1977) listed sago for several lakes where Ca was not detected in the water. Gopal and Kulshreshtha (1980) found that sago tissue contained 438–1,860 times more Ca than the water column. Purohit et al. (1986) also found that a large amount (>44%) of the Ca present in the littoral system (excluding bottom substrate and other biota) can be contained in a macrophyte community dominated by sago. Butler and Hanson (1985, 1986, 1988 unpublished) theorized that, in fresh waters, calcite formation caused by phytoplankton can increase turbidity and cause poor sago growth.

Marl is a complex mixture of clay particles, calcite, trace elements, materials of biological origin, and probably Mg and Fe (Kelly and Ehlmann 1980). It is commonly found on sago (Kollman and Wali 1976) and other *Potamogeton*s (Wetzel 1960), often in lesser amounts in shallow than in deeper water. Oborn (1964) found much Na as well as barium, Co, Fe, K, Mg, Mn, and Sr in the mineral encrustations on sago.

On a large shallow lake in eastern North Dakota, sago in 3–30 cm of water was relatively free of calcareous encrustations; plants in 30–105 cm had thin gray coatings of a flaky texture (Kantrud 1986c, unpublished). However, at the edge of the centrally located area of greatest fetch, where waters were 95–100 cm deep, sago plants in thin stands were covered with a thick reddish coating of a rubbery texture, presumably a mixture of marl and algae. This coating weighted the plants down toward the euphotic zone, which was very shallow because of suspended or colloidal clay particles. It is likely, though, that sago mortality in this central zone was also related to plant age, as the first green sago leaves of the season were seen in this zone, and marl accumulations are directly proportional to plant age (Purohit et al. 1986).

Culture experiments of Huebert and Gorham (1983) showed that sago cannot mobilize enough Mg from the sediments to grow normally. They listed 10 mg/L in the water phase as necessary to meet the Mg requirement. Magnesium can be present in sago tissue at concentrations of 500 times that of the water column and 5,000 times that of the sediments (Gopal and Kulshreshtha 1980). Ho (1979) recorded that the Mg content in sago increased as levels of this element in the water column decreased. Nevertheless, sago occurred in natural waters where Mg was found in very small amounts or could not be detected (McCarraher 1977; Fraser and Morton 1983).

Dissolved O_2 remained high year-round in a polluted lake dominated by sago, except in the most polluted portion where sago did not grow due to high levels of phytoplankton and increased turbidity (Aleem and Samaan 1969a). There, O_2 was completely depleted during summer. Both O_2 consumption and dissolved organic matter (DOM) were lowest year-round where sago was most abundant. Pip (1987) also showed that DOM in waters supporting sago (mean absorbance at 275 nm = 0.29) was significantly lower than in waters free of sago.

In summary, sago tolerates extremes of TDS in the water column. Optimum biomass occurs at 2–15 g/L TDS, but propagule production is greatest at the lower end of this range. The plant may have evolved ecotypes adapted to waters of differing salinity. Sago is characteristic of alkaline waters (pH 7.0–9.0), and has not been recorded in natural waters with pH <6.3 or >10.7. Sago has difficulty mobilizing inorganic C from bottom sediments, and thus favors waters high in CO_3 or HCO_3 ion, with a minimum of 18 mg/L. The plant is often found, and may be monodominant, in oxygen-poor, eutrophic waters, but low nutrient levels alone usually do not limit growth. Sago may have critical requirements for water-column Ca and Mg. The plant tolerates high concentrations of other elements (Table 6).

Temperature

Temperature can be an important variable in growth and niche differentiation among hydrophytes (Auclair et al. 1973; Haller et al. 1974; Wetzel and Neckles 1986). In some years, warmer than normal summer temperatures increase seed germination among annual species, thus accounting for the annual differences in species composition in wetlands (Lundegardh-Ericson 1972). Moderate temperature increases are believed to enhance microbial activity, which leads to increased mobilization of nutrients (Niemi 1975, cited in Keskitalo and Ilus 1987).

Sago grew in deep lakes where summer water temperatures were <12° C (Jimbo et al. 1955), yet produced extremely high biomass in shallow lakes where temperatures reached 31° C (Flowers 1934; Craner 1964; Aleem and Samaan 1969b; Olson 1979). Sago also inhabited a river whose temperature reached 32° C (Carter et al. 1985b). Stuckey (1971) noted that the warm waters tolerated by sago were poorly oxygenated.

Sago is one of the first submersed plants to sprout in spring at temperate latitudes (Moore 1915). Hodgson and Otto (1963) considered 5° C as the lower threshold of sago growth, and Van Wijk (1983) found that 52% of sago turions had sprouted when lake water temperatures reached 5.5° C but concluded, through indoor experiments, that 25° C was optimum for turion germination. Hodgson (1966) showed that at this temperature the carbohydrate reserves in turions were exhausted 16–23 days after germination. Hammer and Heseltine (1988) noted that sago drupelets sprouted and flowering began in Canadian sago when water temperatures reached 8° C and 15° C, respectively. Sago and other submersed plants died in an experimental pond when temperatures reached 38° C (Bourn 1932). Optimum temperature for growth of young sago plants in the laboratory was 23–30° C; growth occured at 10° C, but no leaves were produced; little or no growth occured at 37° C (Spencer 1986a).

Haag (1983) collected drupelets in sediment samples from a large Canadian lake and found that more sago seedlings emerged from sediment in the warmer waters near a power plant than from samples taken in the cooler or deeper waters. Restratification of the drupelets resulted in further emergence of seedlings from the warmwater samples, which suggested that thermal discharge interferes with stratification. The warmer temperatures seemed to have a greater effect on seedling density than did sediment type and depth at the collection sites, probably because of increases in length of the growing season and enhanced seed production. In the lake, sago reproduction was mostly from turions, and seedling survival was minimal. Sago increased in areas affected by thermal pollution near a nuclear power plant on the Finnish coast but, except at shallowest sites, was mostly replaced by *Myriophyllum spicatum* and *Cladophora glomerata* in areas of peak increases in temperature and current velocity (Keskitalo and Ilus 1987). Sago also decreased at another site where a combination of lack of winter ice and increased nutrients allowed several species of algae to prosper.

The seasonal phenology of sago followed mean weekly air and water temperatures more closely than mean sunlight energy, and drupelets matured when air and water temperatures were maximum (Yeo 1965). Spencer's (1986a) controlled experiments suggested that, as long as stored carbohydrates are available from the turions, young sago plants are less influenced by light. This supports the hypothesis that the effects of temperature and irradiance change with sago's growth stage. His study showed that temperature, more than irradiance, affected relative rates of shoot elongation, leaf production, and the production of important pigments. These results indicated that early growth of sago from turions was better suited to cooler waters where carotenoids better protected chlorophyll.

Results of ongoing surveys by the U.S. Bureau of Reclamation (Garrison Diversion Unit Refuge Monitoring Annual Report 1989, unpublished) along the James River, North Dakota and South Dakota, suggest that, in deeper waters, water temperatures during a critical spring period of turion germination and growth can influence peak summer biomass and allocation of resources to propagules. These studies indicate that low water temperatures associated with high water levels during late May to mid-June cause lowered sago biomass but result in the production of heavier turions. Conversely, good turion germination and growth, rapid horizontal deployment of leaves near the water surface, high peak biomass, and increased drupelet production resulted when spring water temperatures were high and water levels were low.

In polluted Wisconsin streams there usually were spring and fall biomass peaks of filamentous algae and a net carbon gain for sago only when water temperatures exceeded 15° C; longer day lengths also likely were required (Madsen 1986). Wong et al.

(1978) also found that when water temperatures reached 18°C, an algae-dominated community began to give way to a sago-dominated community and that, at 23°C, there were few other angiosperms present.

Kiorboe (1980) observed suppressed sago growth in shallow thalassic waters where temperatures approached 25°C and epiphytes covered the plants. Sago generally replaced *M. spicatum* in a Canadian lake in the area with thermal effluent discharge (Dobson 1964, cited by Haag and Gorham 1977). Nevertheless, Madsen (1986) found that sago had maximum net photosynthesis at 25–28°C (T_{opt}) in a Wisconsin stream where the plant was an early-season dominant. This temperature range was lower than for late-season dominants such as *Ceratophyllum demersum* and *M. spicatum*. He suggested that the role of environment or selection in the control of T_{opt} in sago could warrant research because the plant has adapted to a wide range of temperature conditions worldwide.

Sago plants influence the temperature of their own environment. In summer, sago beds shaded bottom sediments and prevented water mixing, which made surface waters warmer in a North Dakota wetland <1 m deep; later in the season, cool surface waters were temporarily stabilized by the sago beds until late fall when surface waters fell through the decomposing plants and complete mixing occurred (Kollman and Wali 1976). Sago beds likely have less effect on water temperature in deeper sites where plants are ineffective in stabilizing bottom soils (Paullin 1973), although it is probable that a thick surface canopy of sago leaves would affect a temperature profile at almost any depth conducive to sago growth (M. G. Anderson, personal communication).

In short, sago's cosmopolitan distribution indicates that the plant has wide temperature tolerance. Temperature has a great regulatory effect on sago growth, phenology, and resource allocation to propagules. Plants have adaptations that allow reproduction under a wide range of temperature extremes and fluctuations. Sago also influences the temperature of the water column, especially in shallow, protected sites.

Water Movement

Wave action greatly reduces the number of species of submersed macrophytes in lacustrine systems (Schiemer and Prosser 1976). Wave action on some large lakes restricts sago and other macrophytes to river inlets and protected bays (Sheffer and Robin-son 1939; Jaworski et al. 1979). It is likely that wave action reduces productivity of *Potamogetons* by direct damage and by the transport of fine nutrient-rich sediments to more sheltered areas (Jupp and Spence 1977b).

Schiemer and Prosser (1976) postulated that a long-term increase in water level from 1.25 m to 1.65 m created sufficient additional wave action that nearly destroyed a formerly wide zone of sago. Nevertheless, sago increased in more sheltered sites by replacing species less prone to mortality from the increased silt accumulations that occurred. Kautsky (1987) showed that sago in sheltered mud bottoms produced about 4 times the standing crop of plants found on exposed sandy and gravelly bottoms. She found that turion production was lower and drupelet production was higher in the sheltered location and postulated that the exposed sites made pollination difficult and caused high mortality of adult plants. An alternative hypothesis is that plants in exposed sites survived by allocating more resources to asexual reproduction (R. G. Anderson, personal communication).

Although sago growth can be limited by severe wave action in shallow waters (Tryon 1954; Boltt et al. 1969; Anderson and Jones 1976; Anderson 1978; Jupp and Spence 1977b), the species often grows well in—or is sometimes even restricted to—deeper portions of wetlands that have a great amount of wave action (Kornas et al. 1960; Downing 1975; Verhoeven 1980a; Clayton and Bagyaraj 1984; Ozimek and Kowalczewski 1984). Wave action in shallow waters tends to erode sediments where plants are rooted, whereas in deeper waters, waves tend to whip and pull the vegetation. Seedlings have difficulty becoming established under such conditions. Turbulence reduces the number of plants found near the center of large bodies of open water but allows considerable growth of individual plants that become established. Spence (1982) stated that it is the depth of the wave-mixed zone that is of great importance to macrophyte distribution in wetlands. The wave-mixed zone is where erosion, sorting, and some particle deposition occur, and the depth and breadth of the zone depend on slope and aspect of the shore and on lake size, principally fetch.

In a brackish coastal lake in New Zealand 22 years after a storm, sago was just beginning to recover; the likeliest causes for failure of plants to regenerate were wave action that removed sediments from the then unprotected lake bottom and increased turbidity due to phytoplankton blooms (Gerbeaux and

Ward 1986). However, sago can prosper after storm damage and increased turbidity have reduced the biomass of other species, but such response is difficult to predict in different wetlands (Ogelsby et al. 1976; Stevenson and Confer 1978; Davis and Carey 1981). Extensive stands of sago can sufficiently stagnate the water column as to reduce phytoplankton production (Aleem and Samaan 1969b).

Dense growths of sago can greatly reduce wave action from winds ≤25 km/h (Putschog 1973; Howard-Williams and Liptrot 1980). But Zaky (1960) showed that winds >29.6 km/h effectively uproot sago and determine its distribution and density in a large (>500 ha) reservoir. In this wetland, sago densities in a protected area were more than 4 times greater than densities in an exposed area. The wind tolerance of sago cannot be stated from these isolated examples; however, Spence (1982) showed that peak wave height at a given wind speed seems to vary with the square root of fetch, and how fetch varies with the width of the water body and irregularities of shoreline as well as with length. He cited an example where plant cover could be as much as 13 times greater on a sheltered shore than on an exposed shore.

Sago has been observed in the plant understory at sheltered sites and in nearly pure stands in more exposed sites (Wilson 1958). Haag (1983) suggested that wave action likely was one of the main restrictions on sago seedling survival in deeper (>2 m) waters in a large Canadian lake where the plant grew mostly as a perennial. In deep (3 m), clear New York waters subject to vigorous wave action, sago plants nearly 3 m long grew from turions borne on tough perennial rootstalks (Moore 1915).

Sago withstands moderate to fast currents but is intermediate in tolerance to turbulence (Butcher 1933; Haslam 1978). Although rated low in anchoring strength compared with other submersed macrophytes, sago is difficult to erode once established (Haslam et al. 1975; Haslam 1978). However, higher current velocities accompanied by increases in depth and turbidity, reduces sago abundance without greatly affecting potential competitors such as *Vallisneria americana* or *Heteranthera dubia* (McConville et al. 1986).

Current speeds >1 m/s were required to limit growth of sago and other macrophytes (Howard-Williams and Liptrot 1980), but sago displaced *Elodea* and *Myriophyllum* at two power plant discharge sites where swift currents were created

(Allen and Gorham 1973). Madsen (1986) found that sago added biomass in a Wisconsin stream even in early April when current velocities reached 2 m/s. Sago prospered and retarded waterflow in canals 10–15 m wide, having flows as high as 13,450 L/s (Corbus 1982).

The common occurrence of sago in flowing waters is attributed to several factors. Van der Voo and Westhoff (1961) found dense sago stands in only 9% of 46 stagnant water areas they investigated, but flourishing stands were present in 24% and 31%, respectively, of 66 river and 13 tidal areas where significant water movement occurred. Sago may survive in flowing water because the plant's narrow leaves enable it to resist silt accumulations (McCombie and Wile 1971). Because of sago's low photosynthetic rate, Westlake (1967) found it difficult to measure increases in photosynthesis of the plant caused by increased water velocity, but found that the rate increased 1.5 times when current velocities increased from 0.2 mm/s to ≥0.4 mm/s. Krausch (1976) postulated that higher sago densities in rivers could be caused by increased contact with nutrients and where there is a lack of annual ice scour.

The degree of water level stability may account for as much as 30% of the annual change in sago abundance (Bellrose et al. 1979). Sago's tolerance to fluctuations seems partly dependent on water clarity and the rate at which the fluctuations occur. Sago withstands water level fluctuations of at least 0.5 to 1.75 m in thalassic waters (Doherty and La Roi 1973; Kulberg 1974; Getsinger et al. 1982; Carter et al. 1985a), and plants can endure periodic exposure under tidal conditions (Kiorboe 1980). The species persisted under fluctuations of at least 1.2 m in clear athalassic waters (Harrison 1962). Sago likely prospered for at least 10 years in a North Dakota lake where water levels fluctuated about 35 cm above and below an average depth of about 70 cm (Kantrud 1986c, unpublished); the plant persisted for decades in a river which fluctuated about 1.0 m (Hunt 1963). Lutz (1960) found no turion production where water was turbid and fluctuated outside a diked area from which carp were removed. Inside a diked area where water levels were stable—and from which carp had also been removed—drupelet production was 280 times greater by weight and 240 times greater by number.

Robel (1962) noted that water-level increases in turbid waters caused sago mortality through light extinction. A water level increase of less than 10 cm

in turbid mixosaline waters resulted in 35% less sago production than the previous year. Similar reductions occurred with 0.4–1.0 m increases in water levels in fresher, less turbid waters (Anderson and Jones 1976; Carpenter 1980). Higher water levels in nutrient-rich lakes favor phytoplankton blooms over sago (Gibbs 1973). Higher water levels sometimes allow ingress of rough fish that caused uprooting and turbidity which lowered sago production (Anderson and Jones 1976). Otherwise, sago production may be increased in sheltered coves due to higher water levels when filamentous algae become less abundant than in shallower water (Anderson and Jones 1976). Sago growth can also increase greatly when higher water levels drown out or otherwise reduce densities of emergent hydrophytes (McDonald 1951).

Purohit (1981) related temporal trends in sago density to changes in water depth in an Indian lake. Sudden increases in water level reduced sago density more in areas where substantial parts of the plants floated than in areas where plants were not tall enough to float. A water level-increase of 1.5 m from June to July destroyed most sago shoots. When water levels were low, sago density declined rapidly as the depth gradient increased. However, when water levels were high, a reverse trend was evident, as the site of maximum sago density shifted towards greater depths. This was caused by the time required for sago to colonize formerly dry shorelines. By the time water levels began to recede in October, sago density was roughly similar across the 0.5–6.5-m depth gradient.

Few other data are available on the effects of lowered water levels on sago. Harris and Marshall (1963) saw great increases in drupelet production in remnant pools of impoundments when water levels were lowered artificially and by evaporation. The greater increases that occurred during the first 2 years of reflooding were suspected to be caused by changes in soil chemistry and nutrient availability. Bailey and Titman (1984) saw sago biomass nearly double as water levels fell 17 cm between growing seasons, even though water clarity was slightly decreased.

Stable water levels allow maximum sago reproduction (Bellrose 1941; Jackson and Starrett 1959; Kuflikowski 1977; Steffeck et al. 1985). Although Low and Bellrose (1944) found greater foliage production of sago in fluctuating water, more drupelets were produced under stable water conditions.

Wind-driven ice (ice scour) can severely damage beds of submersed plants (Martin and Uhler 1939), but I doubt whether ice scour has significant long-term effects on sago because it is resistant to disturbance and has rapid propagule dissemination from established stands. Martin and Uhler (1939) also opined that ice lift would carry away large areas of sago in sluggish streams during spring breakup. In the shallow prairie wetlands of interior North America, it is common in spring to see large amounts of undecomposed sago and bottom sediment lifted to the surface with bottom ice, but I have noticed no long-term changes in sago distribution in these areas. However, Kautsky (1987) mentioned that ice erosion may reduce sago populations in thalassic waters and noticed smallest standing crops at exposed sites. Krausch (1976) felt that lack of winter ice was a factor favoring retention of sago biomass in a river.

In summary, sago is adapted to and highly tolerant of currents and water level fluctuations, and sometimes may be benefited by the increased nutrient supplies and lack of potential macrophyte competitors at sites where water movement is substantial. Presence and abundance, of course, depend on other, often closely associated, environmental factors such as water transparency and sedimentation rates. Sago can survive periodic exposure to air and water level fluctuations of nearly 2 m in clear tidal waters, yet depth increases of as little as 10 cm can greatly reduce production in highly turbid waters. These limits probably are invalid for wetlands with fetches >500 m where an increase in damage from wave action may occur. Sago is moderately tolerant of turbulence caused by wave action, and sometimes prospers after storm damage has reduced populations of other macrophytes. Sago beds can dampen wave action sufficiently to reduce phytoplankton production and likely cause many other biological changes in the littoral.

Bottom Substrate

Texture

Particle size distribution of bottom material is a consequence of water depth and wave action that washes fine particles to sites having less water movement and water energy (Hutchinson 1957; Spence 1964; Sculthorpe 1967). Madsen (1986) pointed out that correlations of sago with substrate can be indirectly related to the wave action or cur-

rents that form the substrates or directly related to the ability of the plant to colonize and maintain root systems in the substrate.

Sago grows on bedrock, as well as on mineral bottoms whose particle sizes range from rubble (Wong and Clark 1976; Pip 1987) to fine clay. It also grows on organic bottoms ranging from peats to mucks. Sago has also been found in limnic (marl) bottoms (Rich 1966; Nichols and Mori 1971; Rich et al. 1971; Haag 1983; Bailey and Titman 1984) and in streams with bottoms of bog iron ore that had disintegrated into sands and gravels (Olsen 1950). Sago frequently occurs in a variety of substrates in a single wetland (Moore 1915; Wilson 1941; Anderson 1978).

Many investigators have mentioned that certain bottom substrates produce higher sago biomass. However, in most of these studies, many other factors could have influenced plant growth. The occurrence of sago in the most common bottom textural classes is shown in Appendix C. Therefore, in this section I will only refer to studies where the production or frequency of occurrence of sago or sago propagules was compared among substrates or related to substrate and other factors.

Schmid (1965) found that sago frequency positively correlated with increased coarseness of bottom substrates. After losses during a tropical storm, sago recovered fastest on a site where the proportion of sand in the top 2.4 cm of bottom was greater than before the storm (Oglesby et al. 1976). Sago was more abundant on both silt and gravel than on sand and more abundant on sandy substrates with gravel than on pure sand in a Wisconsin stream (Madsen 1986). The presence of gravel likely provided a firm environment for roots and decreased the erosional nature of the substrate. In another Wisconsin stream, sago cover was directly related to the amount of sand in the substrate because the plant was better adapted to rooting in sand than the other species found there (Madsen and Adams 1985). Mace et al. (1984) found that sago was common in Wisconsin stream stretches with both Type 1 (sand, gravel, or rubble) and Type 2 (silt) bottoms and suspected that macrophytes in Type 1 stretches obtained nutrients mostly from the water column, whereas those in Type 2 obtained nutrients from the sediments. Sandy, gravelly substrates studied by Kautsky (1987) contained only 40% the density of sago drupelets found in sheltered muds, even though plants in the former substrates allocated 4 times the biomass to reproductive parts. Haag (1983) also observed unfavorable drupelet production and seedling growth on sandy substrates characteristic of turbulent, nutrient-poor conditions. The ability of sago to exploit sandy substrates low in nutrients may relate to benefits provided by mycorrhizas on the root hairs (Clayton and Bagyaraj 1984).

Butcher (1933) and Jensen (1940) indicated that best sago growth occurred where organic-rich silt was deposited on other substrates. Howard-Williams and Allanson (1981) showed that thin (1–2 cm) organic layers are a major source of phosphorus for sago and that long-term transfer of particulate nutrients into deep sands below can be a slow process as long as the sago beds remain intact. Laboratory studies of Peltier and Welch (1969), where sago roots were sealed off from the water column, showed that stem lengths increased faster in natural river sediment than in masonry sand regardless of nutrient content of the water column. In the river from which these plants were collected, sago likely met much of its nutrient demand from silts accumulated in the interstices within the gravel bottom. Ravanko (1972) observed that sago was dominant in sand but was replaced by *Potamogeton perfoliatus* as bottoms became more fine textured.

Silt bottoms are capable of high sago production, and have several times been singled out as especially productive of turions (Wetmore 1921; Craner 1964; Sincock 1965). Ho (1979), nonetheless, rated silt poor for sago production. Silt loams were termed best for sago production by Low and Bellrose (1944). Substrates supporting sago contained more silt and clay than nearby bottoms supporting *Potamogeton crispus* (Rich 1966).

Sago commonly occurs on clays, and such bottoms can be especially productive of turions (Wetmore 1921; Jensen 1940; Craner 1964). Van Wijk et al. (1988) showed that a mixture of 75% washed clay and 25% washed sand was an excellent medium for sago culture. In an African lake, sago grew in monodominant stands where bottoms had the highest (up to 50.9%) clay content (Denny 1972). Sincock (1965), though, found that sago was infrequent on clays and peats compared with sands and silts and suggested that fine clays could prevent adequate rooting. Ordination models of Paullin (1973) placed sago among a group of plants associated with soils containing a low clay fraction and high organic matter content. Anderson and Jones (1976) and Anderson (1978) also rated clays rather poor for sago production compared with sands, silts, and loams, but in the lakes they studied the heaviest soils were subject to the

most wave action. Wetmore (1921) found fewest turions in areas of calcareous hardpan. The probable key to abundant sago production in clays is protection from wave action (Jupp and Spence 1977b). Loams (roughly equal mixtures of sands, silts and clays) have been identified as especially productive of sago (Wetmore 1921; Low and Bellrose 1944; Craner 1964; Anderson 1978; Olson 1979).

Bottom deposits consisting mostly of organic matter in various stages of decomposition are termed fibric (peat), hemic (muck), and sapric (sapropel or gyttja). These often support sago, and McDonald (1951) found that sago was about twice as frequent in bottoms high in organic matter. Nevertheless, Sincock (1965) seldom encountered sago on peats, and Haag (1983) found that the plant was absent for at least 5 years from a site where sediments were highest (27% dry weight) in organic matter, but present for 1 or more years where organic matter ranged from 12% to 26% of dry weight. Table 7 shows the range of organic matter and organic C content in sediments supporting sago.

Several studies indicate that bottom substrate is of little consequence to sago production (Smeins 1967; Van der Valk and Bliss 1971; Olson 1979) or that the plant occurs in a variety of substrates (Pip 1987; Hammer and Heseltine 1988). Sago plants that start from sprouted turions can grow at least 21 days in nutrient solution only (Devlin and Karczmarczyk 1975; Spencer 1986a).

Substrate likely can affect sago's ability to dominate certain sites. For example, in an Indian irrigation area *Vallisneria spiralis* generally replaced sago where bottoms were silty but not in nutrient-poor sandy bottoms (Reeders et al. 1986).

Anderson (1978) found that substrate texture, combined with turbidity and water depth, affected light availability in a large prairie wetland, and he concluded that light intensity limited sago colonization. In his study, firm clays and wave-washed sands found at exposed sites limited high sago production to sheltered shallow bays with peat and sandy-loam soils. Similarly, sago was found throughout the lake studied by Haag (1983), but maximum abundance tended to occur in fine sediments in shallow protected bays.

On a large, shallow (<1.2 m) clay-bottomed lake, sago was also absent from the central area of greatest fetch, but that bottom was not noticeably different from elsewhere in the lake except the narrow swash zone. Instead, the absence of sago in the central zone was attributed to constant turbidity

Table 7. *Extractable compounds and elements in bottom sediments used by sago pondweed.*[a]

Characteristic	Unit of measure	Range or single observation (reference[b])
Nutrients		
Organic matter	%	0.82–28.0 (1;2)
Organic C	%	2.2–9.2 (3;4)
NO_3–N	mg/kg	1.3–5.9 (5;6)
NH_3–N	mg/kg	9.0–65 (6;7)
P	mg/kg	0.4–9100 (8;9)
K	mg/kg	39–453 (5;10)
Other ions and compounds		
Al	mg/kg	1.5–17.5 (8)
Ca	%	0.76–1.24 (8;2)
Cd	mg/kg	20–90 (11)
Cl	mg/kg	7.1–3616 (1;8)
Cu	mg/kg	0.65–48 (1;10)
Fe	mg/kg	15–270 (1)
Li	mg/kg	0.1–22.6 (8)
Mg	mg/kg	31–2991 (1;8)
Mn	mg/kg	6.7–642 (1;8)
Na	mg/kg	60–7080 (1;8)
Ni	mg/kg	0.5–6.0 (8)
Pb	mg/kg	2.0–11.6 (8)
Si	mg/kg	32.5–84.7 (8)
SO_4	%	0.0012–1.99 (1;8)
Sr	mg/kg	6.3–37 (8)
Zn	mg/kg	0.53–791 (1;11)

[a] All measurements on a dry weight basis.
[b] Reference: (1) Olson 1970; (2) Paullin 1973; (3) Neel et al. 1973; (4) Denny 1972; (5) Wilcox and Simonin 1987; (6) Jarvis et al. 1986; (7) Jensen 1940; (8) Kollman and Wali 1976; (9) Fetter et al. 1978; (10) Huebert and Gorham 1983; (11) Adams et al. 1980.

caused by colloidal or suspended clay particles (Kantrud 1986c, unpublished).

I conclude that sago is not substrate-dependent and that its distribution and abundance often depend greatly on wave action and fetch as they affect turbidity and the distribution of soft, easily colonizable sediments. Aversions noted for certain bottom textural classes likely are caused by other factors. Sago from the same locality may have genotypes adapted to different conditions (Kautsky 1987). Recent work by Van Wijk (1988, 1989) and Van Wijk et al. (1988) suggests that these genotypes differentiate freshwater and brackish-water populations, so it would not be surprising if genetic adaptations to substrate types, or the environmental conditions associated with them, were discovered in the future.

Sedimentation and Disturbance

Sediments are moved by wave action to central deeper water areas or trapped by vegetation in peripheral sheltered areas. Beds of submersed aquatic macrophytes in shallow areas of great fetch are likely to be damaged by unstable bottom sediments (Vicars 1976). Plants with feathery surfaces that are easily coated with or weighted down by sediment are at a disadvantage to the linear-leaved sago (Schiemer and Prosser 1976; Vander Zouwen 1982). In openwater areas sago growths can form ring patterns or atolls that formed, according to Varga (1931, cited in Schiemer and Prosser 1976), because of silt deposition in the interior and silt erosion on the periphery.

Although Paullin (1973) thought that sago was ineffective in stabilizing bottom substrates, others (Butcher 1933; Haslam 1978, 1987; Reese and Lubinski 1983) remarked on the species' silt tolerance or ability to consolidate unstable substrates. Madsen and Adams (1985) found that sago was most successful in portions of a Wisconsin stream where growth of other species was limited because of siltation, turbidity, and pollution. Peltier and Welch (1969) saw sago survive 10–30 cm silt deposition in a single season. Sago reached high biomass in silted wetlands (Logan 1975), and Singhal and Singh (1978) considered the species an indicator of siltation. In five water bodies studied by Doherty and La Roi (1973), sago was restricted to the only lake with measurable sediments (3 cm). Sago rhizomes filled an 8–10-cm-thick layer of freshly deposited silt in a single growing season as older rhizomes below died out (Gladyshev and Kogan 1977).

The effects of parent substrate, sedimentation, and decreases in water transparency caused by sediments in the water column are, of course, difficult to separate. Thus Bourn (1932) noted that the great loss of submersed macrophytes in Currituck Sound, North Carolina, occurred almost simultaneously with the sedimentation that resulted from opening and enlarging the Albemarle and Chesapeake Canal. He attributed this loss to the excessive turbidity caused by wind and wave action that kept the fine particulate sediments in almost constant suspension. Bourn believed that only the reestablishment of aquatic plants would return the water to its former clarity.

In heavily silted sites prone to wind-induced turbidity, sago abundance varied greatly with water depth (Jackson and Starrett 1959). Bellrose et al. (1979) documented large losses of sago and other submersed hydrophytes from lakes in the Illinois River valley and concluded that, although altered water levels were locally important, increased turbidity from sedimentation was far more significant.

Otto and Enger (1960) showed that 50–100 ppm suspended natural sediments caused a 50% reduction in weight of cultured sago plants; effects of higher loadings included stem elongation, chlorotic leaves and stems, and apical dominance. Sago was absent from a New Zealand lake where suspended solids measured 100–300 mg/L (Gerbeaux and Ward 1986). Ongoing experiments of Butler and Hanson (1985, 1986, 1988, unpublished) indicate that virtually no sago growth in a lake where concentrations of suspended solids were 40–100 ppm during the growing season. They also found that, even in the absence of fish, resuspension of fine (<5-micron) sediments was sufficient to maintain extreme turbidity.

Sago is a common inhabitant of heavily traveled boat canals, where bottoms are frequently disturbed or dredged (Van Donselarr et al. 1961; Murphy and Eaton 1983; Haslam 1987). Davis and Brinson (1980) placed sago into a group of five species of submersed hydrophytes in North America able to maintain dominance in disturbed ecosystems and considered this consistent with sago's widespread abundance. Sago occurred in wetlands subject to both weed removal and heavy recreational boating (Kaul and Zutshi 1967). Stuckey (1971) also remarked on sago's tolerance to physical destruction by boat traffic. However, sago disappeared where heavy recreational boating disturbed bottom sediments and greatly increased turbidity (Cragg et al. 1980).

Sago drupelets, deeply buried in dark, reducing environments of lake sediments, might be released from dormancy by disturbance (Haag 1983). Haslam (1978) stated that the overwintering propagules of sago are harmed little by soil disturbances common to rivers. Sago was among a group of macrophytes that increased after a river was dredged (Hannan and Dorris 1970).

Logan (1975) attributed good sago growth in silted impoundments to the species' rhizomatous growth form. *Potamogeton* turions can be so firmly embedded in clay bottom substrates that removal is difficult (Jupp and Spence 1977b). However, certain loose mucks may increase sago's susceptibility to disease (Bourn and Jenkins 1928).

In conclusion, the linear growth form of sago leaves is an obvious advantage in sites where broad-leaved species can be weighted down by sediment deposition. Sago's rhizomatous growth form can consolidate silted bottoms, and sago propagules are resistant to disturbance of bottom substrates. Nevertheless, sedimentation and associated turbidity caused by suspended solids can decimate sago populations. Plants can survive up to 30 cm of silt deposition in a single growing season. Suspended sediments >100 ppm during the growing season will lower sago biomass greatly at most sites where the plant grows. Sago can reach high biomass in silted wetlands, but not if fetches are large and silts are often and easily suspended by wave action.

Land Use

Bue (1956) observed little difference in sago frequency in heavily or lightly grazed South Dakota livestock ponds. Yeo (1965) found a dense stand of sago in an irrigation canal heavily grazed by cattle. On Stump Lake, North Dakota, I saw only slightly less sago along heavily grazed compared with ungrazed shorelines, although plants prospered in much shallower water under the latter regime because they were protected by semi-open stands of emergent hydrophytes that grazing had nearly eliminated elsewhere. Barnett (1964) thought the rarity of sago and other submersed macrophytes in a Utah lake was partly attributable to a combination of livestock grazing and carp activity. Here the carp is suspect because *Potamogetons* are generally favored by the effects of domestic livestock on emergent hydrophytes (Duncan and D'Herbes 1982). In the French Camargue, sago is a dominant submersed macrophyte in many grazed marshes, and it also commonly occupies open areas artificially produced by mowing of emergents (Britton and Podlejski 1981). Sago showed a general decrease in frequency in brackish drainage ditches in England's Norfolk Broads when the area was converted from grazing to the production of cereal grains. However, frequency was maintained in an adjacent area where grazing was continued (Driscoll 1986). I conclude that grazing by domestic livestock encourages sago production, except in sites exposed to wave action or those where bottom-feeding fish are present.

Slope

Little information is available on growth of sago on sloping substrates. Nonetheless, the plant seems very tolerant. Boltt et al. (1969) reported it on sandy underwater slopes that angled as much as 31° from the horizontal; they postulated that the absence of several other species from these sites was due to the delicate broad-leaved growth form that increased susceptibility to damage from wave action.

Chemistry

Sago occurs in bottom sediments with salinities of extracted waters up to 24 g/L TDS or conductivities up to 27 mS/cm in inland, likely SO_4-dominated, areas (Smeins 1967; Walker and Coupland 1970; Anderson and Jones 1976; Kollman and Wali 1976; Hammer and Heseltine 1988). These published figures are probably conservative because water-column salinities of up to 104 g/L TDS have been measured in wetlands supporting sago (Ungar 1970). Ungar (1974) cited studies by Flowers (1934) and Flowers and Evans (1966) that showed that sago grows in Cl-dominated bottoms containing >2% salts. Craner (1964) recorded >19 g/L salinity in Cl-dominated sediments 0.3 m deep in wetlands supporting sago.

The salinity of sediments supporting sago is usually higher in the thin oxidized layer at the substrate-water interface than in the reduced layer below it (Kollman and Wali 1976). In a North Dakota wetland, substrate salinity rose slowly during the growing season from 8 g/L to 9 g/L and then rose abruptly to 14 g/L in October (Kollman and Wali 1976). The salinity of the water column also rose during the growing season but fell in October. In Utah wetlands supporting sago, salinities of bottom substrates increased during summer at depths up to 0.15 m but did not change noticeably in deeper strata. No correlations were found between salinities of bottom substrates and production of sago vegetation, turions, or drupelet heads in these wetlands. Instead, production of vegetation and drupelet heads was correlated with salinity of the water column (Craner 1964). Spencer (1987) found that sago turion weight directly related to sediment pH and inversely related to redox potential in California irrigation canals, but turion density was not strongly related to either variable.

Although sago has a poorly developed vascular system (Arber 1920, cited in Stevenson and Confer 1978; Sculthorpe 1967) and absorbs much of its nutrient supply through the leaves (Ho 1979), roots can mobilize all major nutrients (N,P,K) from bottom sediments (Kollman and Wali 1976; Huebert and

Gorham 1983). Table 7 lists some of the chemical constituents found in sediments supporting sago.

Jensen (1940) found that there was NH_3 depletion in bottoms supporting dense sago stands. Haslam (1978) recorded poor correlations between concentrations of this ion and sago distribution; rather, the plant tended to be found in sediments intermediate in NO_3–N. Schiemer and Prosser (1976) found that there was greater sago biomass in soft nearshore sediments higher in N than in shallower offshore sediments. Purohit (1981) also found that the best sago stands were in sediments high in N. Sago was almost always present in Canadian lakes where extracted waters from bottom sediments contained 2.0 mg/L NO_3–N (Hammer and Heseltine 1988). Concentrations of N in sago tissue can be 10–18 times that found in the sediments, but 1,000–5,000 times that of the water column (Gopal and Kulshreshtha 1980).

Sediment P seems especially important for good sago production (Schiemer and Prosser 1976; Jupp and Spence 1977b; Anderson 1978; Haslam 1978). Howard-Williams and Allanson (1981) showed that the upper 5 cm of sediment was a major source of P for an extremely dense (>1,000 shoots per square meter) bed of sago in the littoral of a large wetland where water-column P was low (usually <5 μg/L). In this wetland, competition for P by macroalgae, epiphytic algae, and invertebrates was strong, and little P was transferred to the pure sands below a surface organic layer <2 cm thick. An overabundance of sediment P may increase potential competition from angiosperms, for Peverly (1985) found that P values in sediment and in interstitial water at two sites dominated by sago were lower than at a site dominated by *Elodea canadensis*, *Potamogeton crispus*, and *Fontinalis antipyretica*. Jones and Cullimore (1973) indicated that *Myriophyllum spicatum* is adapted better than sago to wetlands where sediment and water column P both are high. Kollman and Wali (1976) found that P and K content of sediments that supported sago increased constantly during the latter part of the growing season, which they attributed to equilibrium shifts from water to sediment as lake waters became concentrated through evaporation or when organic materials broke down in the sediment. Fetter et al. (1978) found that sago was present in sediments containing up to 9.1 mg/g dry weight P, but submersed plants were absent upstream near a wastewater treatment plant where levels reached 20.6 mg/g. Hammer and Heseltine (1988) found that sago was present in sediments whose extracted waters contained 12 mg/L P. Sago tissue can contain 13–125 times the P concentrations found in the sediments but more than 3,000 times that found in the water column (Gopal and Kulshreshtha 1980).

Anderson (1978) found that sago production, and the proportion of sand in sediments, was negatively correlated with available K in bottom sediments. In his study, sago grew better in substrates with a high sand fraction; the results could have been coincidental or reflected a true aversion of sago to high K concentrations. Haslam (1978) assigned sago to a group of plants found mostly in sediments intermediate in K concentration of the interstitial water. Peverly (1985) found that there were higher K concentrations in both sediment and interstitial water at two stream sites dominated by sago, compared with a site dominated by other submersed macrophytes. Sago occurred in monotypic stands in sediments whose extracted waters contained up to 450 mg/L K (Hammer and Heseltine 1988). Phosphorus in sediments that supported sago increased almost linearly late in the growing season when evaporation occurred, probably because of equilibrium shifts within the water column, which increased many ion concentrations (Kollman and Wali 1976).

Paullin (1973) showed with ordination models that sago tended to occur in wetlands with bottom sediments high in Ca and organic matter, although the plant was among the most widely distributed of all submersed hydrophytes in the area studied. Purohit (1981) also found that best sago stands were in sediments high in Ca and organic matter. Sago showed poorer competetive ability in streams with sandstone (SiO_2), rather than limestone ($CaCO_3$) bottoms, especially in upper sections where plants with lesser nutrient requirements were found (Madsen and Adams 1985).

Haslam (1978) related sago distribution to ionic concentrations of water extracted from riverine sediments; sago tended to be found in sediments low in Mg and intermediate in Ca and SO_4. Correlations between sago distribution and Na concentrations were poor. Gopal and Kulshreshtha (1980) found that sago tissue concentrated Ca and Mg at respective levels of 400 times and 5,000 times that found in the sediments.

In summary, sago grows where salinity (TDS) of waters extracted from bottom substrates is at least 24 g/L. Sago biomass and propagule production seem better related to water-column salinity than to bottom substrate salinity. Sago can tolerate high

levels of various elements and compounds found in bottom substrates (Table 7); most of these have not been proven to limit growth or distribution of the plant. Although sago can mobilize all major nutrients (N,P,K) from sediments, water-column nutrients likely are more important in most wetlands, due to sago's ability to absorb needed nutrients through its leaves. Sago distribution sometimes, however, can be related to concentrations of sediment Ca or Mg.

Communities and Associated Biotic Limiting Factors

Macrophyte

The entire biota of a single water body is sometimes regarded as a single ecological unit (Seddon 1972), and the mere joint occurrence of two species or species groups in a wetland is often interpreted as a positive association (Hogeweg and Brenkert 1969; Pip 1978). However, neither positive nor negative associations imply anything about competition, which is difficult to prove, even in controlled environments. Sago can form discrete beds in the presence of suspected competitors (Denny 1972) and often occurs in wetlands of low species diversity (Mirashi 1954; Howard-Williams and Liptrot 1980; Pip 1987).

Despite differences in the vertical and horizontal distribution of species in a wetland—likely related to competition for light, nutrients, or substrate— an overlapping or mosaic distribution is the rule (Kornas et al. 1960). Submerged vegetation in some lakes may be considered in a state of permanent flux, initiated by chance and controlled by competition (Denny 1973). Maximum sago production only occurs where certain combinations of water chemistry, depth, light transmittance, substrate, and other habitat factors exist. Yet sago coexists with dozens of other species of submersed aquatic plants, both vascular and nonvascular. Sago beds are also frequently interspersed with stands of emergent or floating-leaved hydrophytes (Stewart and Kantrud 1971; Britton and Podlejski 1981; Liston et al. 1981). Some submersed macrophytes that grow in the same wetland with sago are listed in Table 8. Many of the references listed in this table contained information on possible competitive interactions discussed later in this section. Although the information in Table 8 does not reflect a random sample of sago habitat, genera showing high frequency of association with sago include *Myriophyllum, Ceratophyllum, Rup-* *pia, Ranunculus, Chara,* and *Najas,* making them good candidates for the most important worldwide sago competitors. Common members of these genera, like sago, are distributed worldwide and have great environmental tolerance.

Of the 27 species of *Potamogeton* listed in Table 8, only *P. pusillus, P. perfoliatus,* and *P. crispus* probably are important individual competitors of sago in the Northern Hemisphere. In addition, *P. richardsonii* (considered by some to be a subspecies of *P. perfoliatus*) and *P. zosteriformis* likely are important in North America. *Potamogeton richardsonii, P. friesii, P. vaginatus,* and *P. zosteriformis* tend to associate with each other in central North America (Pip 1987) and thus may compete for the same resources.

The wide environmental tolerance of sago is shown by the extensive distributions of the 48 other taxa listed in Table 8. These plants occur in fresh to saline waters of coast and interior in a variety of climates. Waters represented on the right side of the table likely are mostly saline, alkaline, or turbid, whereas those on the left probably are fresh, neutral, or slightly acidic, and clear. Some other submersed macrophytes not shown in Table 8 are often associated with sago. These include the Charophytes *Nitella* and *Tolypella,* the primitive angiosperm *Isoetes,* and many large Chlorophytes.

Sago can alternate in dominance with other species on an annual basis, at least in some wetlands in the glaciated prairie region of North America. There, unstable hydrological conditions cause large fluctuations in salinity of surface waters. In some of the more saline wetlands, dilution of surface waters during periods of relatively high water levels results in dominance by sago (commonly accompanied by *Chara*), whereas evaporative losses can increase salinities so that only the more salt-tolerant *Ruppia maritima* is able to grow (H. A. Kantrud, personal observation). Similarly, some less-saline waters, when diluted, become dominated by less-salt-tolerant macrophytes such as *Utricularia vulgaris* but return to dominance by sago when salinities again increase (Swanson et al. 1988). In addition, plant dominance can be partitioned by other means, including differential timing of the life cycle (Crowder et al. 1977). For example, in India, sago covered its greatest depth range and attained its peak biomass in summer, whereas its most abundant associate, *Hydrilla verticillata,* covered a smaller depth range and attained its peak biomass in the second half of the year (Purohit 1981).

Table 8. Co-occurrences of sago pondweed in the same water body with other vascular submerged macrophytes and Chara in areas throughout the world.

Species (number of occurrences)	References[a] (number of species)																															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
	(25)	(22)	(19)	(19)	(17)	(16)	(15)	(15)	(14)	(14)	(14)	(14)	(14)	(14)	(14)	(13)	(13)	(12)	(12)	(12)	(12)	(11)	(11)	(10)	(10)	(9)	(9)	(9)	(9)	(9)	(8)	(8)
Potamogeton pectinatus (96)	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Myriophyllum spp. (65)	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Ceratophyllum demersum (47)	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Ruppia spp. (44)	X	X			X	X	X			X		X		X	X	X					X			X						X		
Chara spp. (41)	X		X	X	X	X	X	X	X	X	X	X	X	X	X	X	X		X	X	X	X	X	X	X	X	X	X	X			
Najas spp. (35)	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X					X	X		X	X	X	X					
Ranunculus spp. (31)	X	X	X	X	X	X	X	X	X	X					X			X	X	X	X	X	X	X	X	X	X	X		X		X
Zannichellia spp. (31)	X	X	X	X	X	X	X	X	X					X	X	X		X	X	X	X	X	X	X	X			X		X		
Elodea spp. (28)	X	X	X	X	X	X			X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X		X	X					X
Potamogeton richardsonii (26)	X	X	X	X	X		X	X	X	X	X	X	X	X	X	X	X	X	X		X		X			X	X	X	X			X
Potamogeton pusillus (25)	X	X	X			X	X	X	X	X			X	X	X	X	X	X			X	X	X	X		X		X				X
Potamogeton zosteriformis (21)	X	X		X	X	X	X	X	X	X	X		X	X	X	X	X	X				X				X		X		X		
Potamogeton crispus (19)	X							X	X	X	X	X		X	X			X	X	X		X		X	X			X			X	
Potamogeton perfoliatus (18)	X							X	X	X								X	X	X				X			X				X	
Vallisneria spp. (17)	X		X	X								X	X	X	X	X							X	X	X		X					
Utricularia spp. (15)	X				X		X		X		X		X	X		X	X	X			X	X	X			X	X	X				
Potamogeton natans (15)	X	X	X	X	X	X							X		X	X	X	X				X	X			X						
Potamogeton foliosus (12)	X	X	X	X	X		X	X			X			X	X	X		X			X	X										
Potamogeton illinoensis (10)	X	X	X	X	X								X	X	X	X	X						X									
Potamogeton amplifolius (10)	X	X	X					X	X	X	X	X		X				X	X	X				X								
Callitriche spp. (10)	X	X	X			X	X		X	X								X	X	X	X			X								
Potamogeton praelongus (10)	X	X	X	X	X	X						X		X		X						X				X				X		
Heteranthera dubia (10)	X		X	X	X		X	X				X	X	X	X	X	X	X				X	X			X						
Potamogeton nodosus (9)		X		X	X	X	X	X			X		X												X					X		
Zostera spp. (8)																																
Potamogeton gramineus (8)	X		X	X			X		X	X	X											X							X			
Potamogeton friesii (6)	X	X	X	X	X	X												X													X	
Hippuris vulgaris (5)				X							X						X						X									
Potamogeton lucens (5)									X	X									X									X				
Potamogeton vaginatus (5)	X						X									X					X											
Potamogeton filiformis (5)												X																				
Potamogeton obtusifolius (5)			X			X		X	X	X				X	X			X		X		X			X		X					
Potamogeton epihydrus (5)	X	X	X	X	X				X									X		X		X										
Potamogeton spirillus (3)	X	X	X																													

[a] (number of species)

Table 8. *Continued.*

References[a] (number of species)

Species (number of occurrences)	1 (25)	2 (22)	3 (19)	4 (19)	5 (17)	6 (16)	7 (15)	8 (15)	9 (14)	10 (14)	11 (14)	12 (14)	13 (14)	14 (14)	15 (14)	16 (14)	17 (13)	18 (13)	19 (13)	20 (12)	21 (12)	22 (12)	23 (11)	24 (11)	25 (11)	26 (10)	27 (10)	28 (9)	29 (9)	30 (9)	31 (8)	32 (8)
Potamogeton robbinsii (3)	x	x																														
Potamogeton alpinus (2)																		x														
Potamogeton densus (2)						x	x																									
Littorella uniflora (2)																			x													
Potamogeton maackianus (2)			x																	x												
Isoetes spp. (1)	x																															
Potamogeton trichoides (1)										x																						
Potamogeton strictifolius (1)																																
Potamogeton helveticus (1)																	x															
Hydrocharis morsus-ranae (1)																			x									x				
Potamogeton malaianus (1)																																

Species	33 (8)	34 (8)	35 (8)	36 (8)	37 (7)	38 (7)	39 (7)	40 (7)	41 (7)	42 (7)	43 (6)	44 (6)	45 (6)	46 (6)	47 (6)	48 (6)	49 (6)	50 (6)	51 (6)	52 (6)	53 (6)	54 (5)	55 (5)	56 (5)	57 (5)	58 (5)	59 (5)	60 (5)	61 (5)	62 (5)	63 (4)	64 (4)
Potamogeton pectinatus	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Myriophyllum spp.	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x		x
Ceratophyllum demersum	x	x	x	x					x	x	x	x	x	x	x	x	x	x				x	x		x	x	x				x	
Ruppia spp.		x			x		x	x	x	x	x						x		x	x				x		x				x		x
Chara spp.		x	x	x	x		x			x	x			x	x		x	x		x	x			x		x				x		x
Najas spp.		x	x	x					x	x																	x		x			
Ranunculus spp.	x		x	x										x					x	x	x		x				x		x		x	
Zannichellia spp.	x	x	x	x			x					x		x		x			x											x		
Elodea spp.		x	x						x						x			x			x				x							
Potamogeton richardsonii	x			x	x			x									x												x			
Potamogeton pusillus		x	x	x	x		x									x						x								x		
Potamogeton zosteriformis	x							x	x						x	x																x
Potamogeton crispus		x									x	x						x	x	x	x			x	x		x	x				
Potamogeton perfoliatus				x				x	x	x	x	x						x	x								x	x			x	
Vallisneria spp.						x		x	x	x													x		x							
Utricularia spp.	x	x													x		x										x					
Potamogeton natans													x																			
Potamogeton foliosus										x																						
Potamogeton illinoensis	x																															
Potamogeton amplifolius									x						x																	
Callitriche spp.																x																

Table 8. Continued.

References[a] (number of species)

Species (number of occurrences)	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64
	(8)	(8)	(8)	(8)	(7)	(7)	(7)	(7)	(7)	(7)	(7)	(6)	(6)	(6)	(6)	(6)	(6)	(6)	(6)	(6)	(6)	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(4)	(4)
Potamogeton praelongus															x																	
Heteranthera dubia			x																													
Potamogeton nodosus		x	x																							x						x
Zostera spp.					x																											
Potamogeton gramineus				x																												
Potamogeton friesii		x																												x		
Potamogeton lucens													x																			
Potamogeton vaginatus								x																								
Potamogeton filiformis							x																									
Potamogeton spirillus						x																										
Potamogeton robbinsii (3)																									x							
Hydrilla verticillata												x										x		x								
Potamogeton maackianus (2)					x																	x	x									
Potamogeton schweinfurthii (2)						x																										
Ottelia alismoides (1)																						x										
Potamogeton × bunonyiensis (1)																						x										
Potamogeton monogivus (1)																																

Species	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96
	(4)	(4)	(4)	(4)	(4)	(4)	(4)	(4)	(4)	(4)	(3)	(3)	(3)	(3)	(3)	(3)	(3)	(3)	(3)	(3)	(3)	(3)	(2)	(2)	(2)	(2)	(2)	(2)	(2)	(2)	(2)	(2)
Potamogeton pectinatus	x	x	x		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Myriophyllum spp.		x			x		x	x	x	x	x			x		x			x	x	x	x					x	x		x	x	x
Ceratophyllum demersum			x																													
Ruppia spp.	x					x	x		x			x			x		x	x	x	x	x				x	x	x	x				
Chara spp.		x	x		x		x	x		x				x			x		x	x		x		x								
Najas spp.																	x	x														
Ranunculus spp.						x		x								x													x			
Zannichellia spp.	x				x				x					x	x																	
Elodea spp.		x		x																												
Potamogeton pusillus				x																												
Potamogeton crispus																																
Potamogeton perfoliatus																							x									
Vallisineria spp.													x																			

Table 8. *Continued.*

Species (number of occurrences)	References[a] (number of species)																															
	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96
	(4)	(4)	(4)	(4)	(4)	(4)	(4)	(4)	(4)	(4)	(3)	(3)	(3)	(3)	(3)	(3)	(3)	(3)	(3)	(3)	(3)	(3)	(2)	(2)	(2)	(2)	(2)	(2)	(2)	(2)	(2)	(2)
Potamogeton natans		x	x																													
Potamogeton illinoensis													x																			
Zostera spp.	x											x																				
Hippuris vulgaris											x																					

[a] References: (1) Crowder et al. 1977; (2) Pammel 1917; (3) Wilson 1941; (4) Volker and Smith 1965; (5) Metcalf 1931; (6) Mathiesen and Nielsen 1956; (7) Olson 1979; (8) Stewart 1962; (9) Paullin 1973; (10) Ozimek 1978; (11) Fraser and Morton 1983; (12) Neel et al. 1973; (13) Oberholzer and McAtee 1920; (14) Hunt 1963; (15) Lind and Cottam 1969; (16) Rickett 1924; (17) Downing 1975; (18) Thomson 1944; (19) Lachavanne 1979; (20) Jupp et al. 1974; (21) Stewart and Kantrud 1971; (22) Nichols and Mori 1971; (23) Sigler 1948; (24) Carter et al. 1985a; (25) Verhoeven 1980a; (26) Van der Valk and Bliss 1971; (27) Rickett 1922; (28) Olsen 1950; (29) Anderson and Jones 1976; (30) Wallentinus 1979; (31) Kadono 1982; (32) Reynolds and Reynolds 1975; (33) Swindale and Curtis 1957; (34) Nelson 1954; (35) Bellrose 1941; (36) Barker and Fulton 1979; (37) Jimbo et al. 1955; (38) Billore and Vyas 1981; (39) Jensen 1940; (40) Bergman 1973; (41) Moore 1915; (42) Bourn 1932; (43) Davis and Carey 1981; (44) Singh 1981; (45) Vass 1980; (46) Kornas et al. 1960; (47) Schmid 1965; (48) Smeins 1967; (49) Hammer et al. 1975; (50) Merry et al. 1981; (51) Ravanko 1972; (52) Jerling and Lindhe 1977; (53) Brooker and Edwards 1973; (54) Denny 1973; (55) Boltt et al. 1969; (56) Singhal and Singh 1978; (57) Adams et al. 1980; (58) Verhoeven and Van Vierssen 1978a; (59) Schiemer and Prosser 1976; (60) Janauer 1981; (61) Disrud 1968; (62) Sterling 1970; (63) Jenkin 1936; (64) Verhoeven 1980a; (65) Martin and Uhler 1939; (66) McCombie and Wile 1971; (67) McCarraher 1972; (68) Tryon 1954; (69) Kiorboe 1980; (70) Verhoeven 1975; (71) Lundegardh-Ericson 1972; (72) Getsinger et al. 1982; (73) Verhoeven 1980a; (74) Anderson 1950; (75) Leah et al. 1978; (76) Ward 1976; (77) Adams et al. 1973; (78) Robel 1961b; (79) Klavestad 1957; (80) Natelson 1954; (81) Aleem and Samaan 1960a; (82) Smith 1946; (83) Howard-Williams and Liptrot 1980; (84) Bailey and Titman 1984; (85) Verhoeven and Van Vierssen 1978b; (86) Congdon and McComb 1976; (87) Zhadin and Gerd 1961; (88) Robarts and Allanson 1977; (89) Critcher 1949; (90) Ungar et al. 1969; (91) Chapman 1960b; (92) McCarraher 1977; (93) Thorne-Miller et al. 1983; (94) den Hartog and Segal 1964; (95) Seddon 1972; (96) Crum and Bachman 1973.

Sago frequency showed a bimodal depth distribution in an African lake where *Chara* dominated the depths between the modal peaks (Denny 1972). Gibbs (1973) described a curious cycle that followed a drought that eliminated all surface water in a shallow (<85 cm) New Zealand wetland. Emergent macrophytes germinated and a sparse sago stand survived in wet ooze. When 50–60 cm of water was replenished, *Chara* was dominant for more than a year but suddenly decayed with the onset of a phytoplankton bloom. That, in turn, diminished and allowed *Chara* to recover and then be replaced by a vigorous growth of sago and *Potamogeton crispus* at water depths nearly identical to those that had supported the *Chara*. Reduced water transparency caused by the phytoplankton bloom largely explained the first decline in *Chara*, but not the replacement of *Chara* by *Potamogeton*s. Gibbs (1973) stated that the balance between phytoplankton, macroalgae, and macrophyte dominance in this wetland was delicate.

Seasonal abundance of sago in two Wisconsin streams illustrated sago's ability to take advantage of the phenology of suspected competitors while simultaneously occupying stressed environments (Madsen and Adams 1985). In one stream, sago had highest relative cover in May before *Elodea canadensis* and other species began rapid growth, but in upper stream sections sago was not found to coexist with plants having lower nutrient requirements. In the other stream, sago increased in dominance in July after the senescence of *P. crispus*. In the lower sections of both streams, sago maintained dominance in areas of pollution, siltation, shifting sands, and increased turbidity.

Sago is rare or absent in some waters for unknown reasons. As discussed earlier, however, it is well documented that sago does poorly when growing in the same wetland with specialist taxa of acidic, nutrient-poor waters (Pip 1984) where free CO_2 is the only carbon source (Hinneri 1976) or where calcium is mostly unavailable (Hutchinson 1975). The probable competitive advantage of sago generally occurs at high, but not extreme, values for common water chemistry parameters that include TDS, pH, total alkalinity, Cl, SO_4, Kjeldahl N, and P (Pip 1987; Hammer and Heseltine 1988). Other physical factors often present at sites where sago seemingly lacks competitive ability include increased water levels (Harris and Marshall 1963; Boltt et al. 1969) and very soft (Ravanko 1972) or exposed, coarse-

grained bottom substrates (Purohit 1981). Other *Potamogeton*s and members of the genera *Ceratophyllum*, *Myriophyllum*, *Chara*, and *Ruppia* were usually the main sago associates in these instances. Factors likely related to sago competition and succession are included in the following paragraphs, but declines or increases in plant abundance often are related to factors so completely interrelated that synergistic effects may be the best possible explanation for such events (Carter and Rybicki 1986).

The distribution of sago and other submersed macrophytes within some wetlands likely is determined by a combination of habitat factors and differences in the biology of the plants themselves. Thus, the inability of sago to grow well with *Zannichellia palustris* and *Ranunculus baudotii* in the shallower portions of a group of wetlands studied by Van Vierssen and Verhoeven (1983) could be attributed to sago's lesser abilty to produce viable diaspores in areas subject to desiccation, whereas the inabilty of the two other species to coexist with sago in the deeper portions of many ponds could be attributed to the higher levels of chlorinity found there.

Schiemer and Prosser (1976) studied an Austrian lake inhabited by sago and *M. spicatum*, which occupied a much greater area than sago. Exceptions were a narrow zone of greatly increased silt deposition—where sago likely was more competitive because it is better able to resist coatings of silt and epiphytic algae which cause loss of buoyancy—and again, in more windswept portions of the lake—where sago, unlike *M. spicatum*, was able to anchor itself to the firm substrates found there. Sago and *Ceratophyllum demersum* increased 2 times and 8 times in absolute frequency, respectively, in a Wisconsin lake as *M. spicatum* declined for unknown reasons (Carpenter 1979).

Haag and Gorham (1977) saw *Elodea canadensis* begin seasonal growth earlier in an area of thermal effluent discharge on a large Alberta lake, and then shade out or suppress the early growth of sago and other submersed macrophytes. By July though, storm damage and self-shading by *Elodea* weakened it sufficiently to produce thinning, which let the current year's growth of sago reach maximum standing crop by mid-August. An early-sprouting stand of *Najas* seemed to shade out sago in deeper waters of an Ohio impoundment following winter drawdown, but sago was more abundant at shallower sites than before the drawdown (Gorman 1979).

Sago can replace other macrophytes under certain conditions. McDonald (1951, 1955) reported that sago succeeded *Utricularia* after *Typha* mortality in a Michigan wetland. He postulated that if the *Typha* were to recover, sago would decline rapidly. Baldwin (1968) reported that an initial community dominated by *Chara* sp. would be replaced by a sago–*Najas* community in freshwater impoundments in the southeastern United States, but that succession to a *Utricularia–Cabomba–Ceratophyllum* community would occur if alkalinity were not maintained. Sago's rapid growth rate allows it to quickly occupy large water surfaces and smother potential competitors. This may be one reason sago often is not found with a diversity of species (Meriaux 1978).

Sago, *M. spicatum*, and *Hippuris vulgaris* replaced *Najas*, *Chara*, and other *Potamogetons* as an English lake high in Cl became eutrophic (Leah et al. 1978). Filbin and Barko (1985) suggested that competition for nutrients may be reduced when sago grows with poorly rooted species.

Sago does not occur with *Ruppia* spp. in polysaline to hypersaline marine lagoons where water level fluctuations are severe, but in mixosaline (5,400–16,200 mg/L) estuaries with more stable water regimes, sago can easily displace *Ruppia* (Howard-Williams and Liptrot 1980; Verhoeven 1980a). This is attributed to sago's larger number of better adapted diaspores and the rapidity with which it fills both the substrate and water column. Verhoeven (1980a) stated that the autecology of sago and its competetive relations with *Ruppia* in fresh and slightly brackish waters need further study.

Dense floating beds of *Chara* that are independent of bottom substrate were observed to shade out, but not eliminate, sago in African wetlands (Denny 1973). In a Michigan wetland dominated by *Chara*, sago survived only at a stream inlet (Rich et al. 1971). Bolen (1964) thought that the physical preponderance of unbroken carpets of *Chara* and *Ruppia maritima* growing at near optimum salinities would allow little chance for sago or other aquatic plants to establish in Utah wetlands. In shallow sites, sago seedling mortality may be high from damage caused by semi-floating masses of plant material and burial by litter (Haag 1983).

Plants with large floating or semi-erect leaves, such as *Nelumbo lutea*, can kill sago by shading (Bellrose 1941), but sago can survive fairly dense emergent growth (Wilson 1958). Shading by large algae can also occur in marine waters

(Ravanko 1972). Trees growing along streams can also greatly reduce sago biomass through shading (Madsen 1986).

Cohen et al. (1986) planted *Myriophyllum exalbescens* (*M. spicatum*) and sago together in aquaria and clipped stems to simulate grazing. Results of this experiment suggested that sago can be displaced by *M. spicatum* under competition for light because sago reacted to clipping by growing new shoots from roots, whereas *M. spicatum* grew new stems below the point of clipping. Similar abilities by other plants could be expected to adversely affect sago. Conversely, mechanical harvesting of a sago–*Potamogeton pusillus* community resulted in an increase in the much shorter *Heteranthera dubia* (Engel 1984). In this case, the taller *Potamogeton* community obviously could out-compete *H. dubia* for light.

A natural succession of submersed macrophytes is often seen in newly constructed reservoirs. In such a reservoir with stable water levels in Czechoslovakia, sago appeared as the wetland was filling, but populations showed no strong expansion until 5 years later, when populations of *Elodea canadensis*, *Utricularia australis*, and *Lemna* sp. had decreased considerably (Krahulec et al. 1987). Rapid replacement by sago and other *Potamogetons* of an initial growth of *Utricularia* was also noted by Henry (1939) in a newly flooded impoundment in North Dakota. Steenis (1939) saw the aggressive *P. foliosus* (which rapidly spreads when shoots break away and grow) thwart efforts to establish sago on some newly flooded wildlife refuges in the northern Great Plains, but sago became dominant as the impoundments aged.

Almost all hydrophyte communities deposit organic matter and trap mineral materials, so hydrarch succession normally proceeds towards less hydric habitat and submersed plants are succeeded by emergents (Walker 1959b; Jahn and Moyle 1964; Whitman 1976). Thus, the presence of emergent plants in and around sago beds can indicate such succession (Van Donselarr et al. 1961; Meriaux 1978; Verhoeven 1980a). Verhoeven (1980a) suggested that, in thalassic waters, such succession was restricted to waters where salinities are less than 9 g/L. Similarly, I have noted no large accumulations of organic matter in mesosaline wetlands of the North American prairies, where sago is often monodominant, but have seen hundreds of instances where sago and other submersed species were eliminated by succession to *Typha* monotypes in

fresher wetlands where organic matter increased. Lack of fire and grazing and the spread of the *Typha angustifolia* or hybrid *Typha* likely was implicated in the buildup of organic matter (Kantrud 1986b,c, unpublished). Siltation from adjacent cropland can reduce water depth and encourage emergent vegetation in such wetlands. Vermaak et al. (1981) observed that sago rapidly replaced communities of emergent hydrophytes in the littoral zone of an oligosaline lake when its acidic waters (pH 4.5) were turned circumneutral. I assume, then, that succession back to emergent growth would occur if conditions were reversed.

I conclude that sago is often found with a large variety of submersed and emergent angiosperms and macroalgae, but it has a marked tendency to occur in discrete beds in stressed environments or those high in ionic content and pH. Sago can alternate in dominance with other species seasonally and annually and show bimodal depth distribution in a single wetland. The competitive abilty of sago seemingly is enhanced by its phenoplasticity, leaf morphology, pollution tolerance, and ability to rapidly colonize unoccupied habitats. However, sago likely is at a disadvantage in acidic, Ca- or mineral-poor sites; sites subject to hypersalinity and water-level fluctuations; and those dominated by nonrooted species or species with large floating or semi-erect leaves. Replacement of sago by emergent plants is common in nearshore zones subject to deposition of organic and mineral matter, often as a result of man's use of uplands in the watershed.

Algal

Growth of submersed macrophytes directly affects their associated periphytic algal communities. The seasonal changes in algal types found by Morin and Kimball (1983) on *Myriophyllum heterophyllum* undoubtedly holds true for many other species of submersed angiosperms. Sago is often found with *Cladophora, Enteromorpha, Fragilaria, Nodularia, Oedogonium, Pediastrum, Rhizoclonium,* and *Spirogyra,* particularly in small wetlands or sheltered areas (Huntsman 1922; Martin and Uhler 1939; Rich 1966; Schiemer and Prosser 1976; Marvan and Komarek 1978; Howard-Williams 1981). Ulvaceae and *Chaetomorpha* were found with sago in oligohaline to mesohaline marshes in the French Camargue (Britton and Podlejski 1981). Such algae can suppress sago growth during summer months by shading and crushing (Ozimek et al. 1986) and may lower sago's resistance to burrowing invertebrates (Prejs 1986a,b, 1987).

I saw sago growth and drupelet production severely limited, likely due to shading by filamentous algae, along exposed shorelines in waters <30 cm deep in West Stump Lake, North Dakota. Beyond that depth, sago prospered even though much filamentous algae was draped around the stems below the leafy branches, and benthic algae carpeted the bottom. Such algae may actually have benefitted sago through reductions in water turbidity.

Epiphytic algae and a host of small plants and animals use sago as a substrate in inland waters. Wisconsin sago was higher in algal aufwuchs than four other genera of aquatic macrophytes (Gough and Woelkerling 1976). Sago epiphytes in a Wisconsin impoundment weighed more than the sago itself (Filbin and Barko 1985). Epiphyte biomass on sago in a Manitoba wetland varied from 48.6 g C/m_2 in high-density sago stands to 11.8 g C/m_2 in low-density stands (Hooper and Robinson 1976). However, Hynes (1970) observed little epiphytic development on sago in streams, and Marvan and Komarek (1978) observed little development of epiphytes on living sago where filamentous algae were common.

Sago epiphytes also vary in abundance in thalassic waters. Kornas et al. (1960) found that epiphytic algae was rare on sago along the Baltic seacoast but adnate coelenterates were common. Epiphytes were seen by Lundegardh-Ericson (1972) only on sago growing in the deepest part of Baltic coves. Staver et al. (1981) estimated sago biomass to be 100–200 times that of the associated epiphytes in Chesapeake Bay in the United States. In contrast, Kiorboe (1980) in Finland and Kollar (1985) in Chesapeake Bay observed epiphytes so abundant as to suppress sago growth. A complex of epiphytes developed on sago leaves at an early stage of growth in a South African estuarine lake (Howard-Williams et al. 1978; Howard-Williams and Liptrot 1980); these algae may have helped sago absorb phosphorus (Howard-Williams and Allanson 1981).

Much remains to be learned about the effects of epiphytes on sago. Sago leaves 1.5 weeks old can be colonized by epiphytes, and cuticular damage can occur at 6 weeks (Howard-Williams et al. 1978). Cattaneo and Kalff (1980) and Moss (1981) suggested that plants like sago with undissected leaves are not conducive to epiphyte growth. Lesser

epiphytic growth may allow survival in relatively eutrophic waters. With sago, it is usually difficult to separate true epiphyton from material that is simply entangled in stems and leaves or associated with calcareous coatings. Oborn (1964) attributed calcite deposition on sago to the bacterium *Bacterium precipitatum* and also found various desmids and diatoms in the calcite.

Some submersed angiosperms, including at least one *Potamogeton*, inhibit the growth of certain phytoplankton (Hasler and Jones 1949; Hegrash and Matvienko 1965). Fitzgerald (1969) showed that some submersed macrophytes and filamentous algae commonly found in sago-inhabited waters remained relatively free of epiphytes in nitrogen-limited culture, and that epiphytic growth on a common filamentous alga (*Cladophora* sp.) was related to conditions of surplus nitrogen compounds in the water column. He proposed that submersed macrophytes prevented the growth of epiphytes by competition when nitrogen is limited. However, bacteria-sized organisms that have selective toxicity to some algae were also found, so both nitrogen levels and toxins may have been involved in the epiphyte suppression. Hooper-Reid and Robinson (1978a,b) listed epiphytic algae and diatoms found at a sago-dominated site in a prairie wetland in Manitoba and found that this site had more physiological indicators of nutrient deficiency for the algae than did a nearby site dominated by emergents.

Phytoplankton are often abundant in sago-inhabited waters and cause great increases in turbidity which can drastically lower production of sago, restrict it to shallow (<35 cm) waters, or render its habitat completely unsuitable (Crum and Bachman 1973; Andersen 1976; Filbin and Barko 1985). Phytoplankton can be moved by wind and affect different areas of a wetland (Jenkin 1936). Martin and Uhler (1939) stated that decomposing blue-green algae weakened sago, but they gave no direct evidence. It may be normal for submersed angiosperms to alternate in dominance with phytoplankton in many lakes of intermediate depth, although the reasons for these changes are unknown (Mitchell 1971). Harrison (1962) opined that alternating sago and algal blooms were related to irregular scouring of a lake bottom by high water levels. Increased phytoplankton abundance has also been implicated in a shift in dominance from submersed to emergent hydrophytes (Niemeier and Hubert 1986).

Gorman (1979) proposed a long-term model of autotroph succession based on observations in a eutrophic, sago-inhabited impoundment in Ohio. A spring bloom of phytoplankton occurred when water levels were slightly deeper, followed in the next year by a summer increase in macroalgae after a partial winter drawdown. Both of these pathways led to partial or complete elimination of submersed angiosperms. Observations of Butler and Hanson (1985, 1986, 1988, unpublished) suggest that light-limiting blooms of *Fragilaria* in a Minnesota sago lake result from overgrazing of zooplankton by fish.

Sago can die-back early in the growing season, concurrent with extensive blooms of *Gleotrichia*, *Anabaena*, and *Aphanizomenon* in waters rich in P (Welch et al. 1979). Leah et al. (1978) recorded that high summer populations of *Apanothece*, *Coelosphaerium*, *Lyngbya*, and *Anabaenopsis* in P-rich waters where sago, now found in small amounts, was probably more abundant before eutrophication. Van Vierssen and Verhoeven (1983) also associated reduced coverage by macrophytes, primarily sago, to decreased light penetration caused by phytoplankton blooms in P-rich waters. Kaumeyer et al. (1981) estimated sago biomass to be only about twice that of phytoplankton in Chesapeake Bay in the United States. Nevertheless, phytoplankton production can be greatly reduced in portions of polluted lakes where sago is abundant (Aleem and Samaan 1969a). Chlorophyll *a* concentrations can be 80% lower in beds of sago and other submersed macrophytes than in nearby openwater areas (Godshalk et al. 1987). Sago growth reached maximum values when algal populations and chlorophyll concentrations fell to lower levels in a eutrophic South African wetland having a seasonal water regime (Coetzer 1987). The algal standing crop (excluding nano-algae and cyanophytes) seemed to be limited by turbidity associated with high water levels.

In summary, sago coexists with a wide array of periphytic and planktonic algae that change seasonally with sago biomass. Periphyton can lower sago biomass by shading, especially in shallow, sheltered locations, but some epiphytes may help sago assimilate P. Phytoplankton often seriously limit sago biomass through reductions in water transparency, and blooms likely can be caused by a variety of factors, including eutrophication, water-level fluctuations, storm damage, and imbalances in the trophic structure. The relations between algal populations and submersed angiosperms need further research.

Organic Pollutants

Sahai and Sinha (1976) surveyed portions of an Indian lake, unpolluted and polluted (with human sewage and detergents), and found that sago net annual production was reduced >90% in some areas of the polluted part. Those areas had low O_2 and high levels of free CO_2 from decomposition of organic materials, and the growth period of sago was also reduced in these areas. Ozimek (1978) found an extremely leafy (var. *scoparius* Wallr.) sago in Polish wetlands heavily polluted with sewage. Plants did not flower and began dying much earlier than the variety of sago common to the area. In polluted French wetlands, a peculiarly thin growth form of sago was found by Meriaux (1978). Organic muds rich in H_2S probably cannot support rhizomatous plants (Verhoeven 1980a). Fetter et al. (1978) found that sago was present and absent at sites with BOD's (biochemical oxygen demand) of 5.4 and 26.9 mg/L, respectively, and coliform bacterial counts of 478/mL and 3,470/mL.

Coatings

Bourn (1932) found that the hydroid *Cordylophora* suffocated and injured sago and formed gelatinous coatings inhabited by other harmful organisms. Coatings found on sago by Schiemer and Prosser (1976) were composed of silt and the mucilaginous epiphytic diatom *Cybella prostrata*; these coatings shaded assimilating parts and increased plant weight. I found sago plants near the center of West Stump Lake, North Dakota, covered and weighted down by reddish rubbery coatings almost 1 cm in diameter. Under a microscope, these coatings looked like a mixture of marl, bacteria, epiphytes, and clay particles. In this zone, sago growth and drupelet production were suppressed, but the zone was surrounded by a contiguous stand of healthy sago. I attributed the formation of the coatings to the extremely fine clay particles held in suspension in the portion of the lake where fetches were greatest. These particles likely accumulated on the normal leaf marl and formed a substrate for microbiota.

Diseases and Parasites

Vast areas of sago and other submersed hydrophytes were lost in Virginia and North Carolina wetlands from 1918 to 1926. Bourn and Jenkins (1928) believed that a disease caused by an aquatic strain of the fungus *Rhizoctonia solani* was responsible for the decline. They found that sago growing in muck soils in water of intermediate salinity (3–7 g/L) was most vulnerable to the disease. Another sago decline occurred in this area in 1961. Various fungi and bacteria were isolated from random samples of sago taken from this area, and several of the fungi were also inoculated into seemingly healthy plants by Lumsden et al. (1963). They found the fungi *Pythium* spp., *R. solani*, *Curvularia* sp., *Phoma* sp., *Pullularia pullulans*, *Hyaloflorae* sp., and other miscellaneous fungi and bacteria on sago, and they concluded from the inoculation studies that although *R. solani* is pathogenic to sago under certain environmental conditions, one or more species of *Pythium* may have been responsible for the decline. Teeter (1963) found that the fungus *Tetramyxa parasitica* was associated with deformities of sago rhizomes and turions cultured from plants taken from Utah wetlands. It cannot be concluded from any of these studies that sago is particularly vulnerable to disease or that pathogens are the direct cause of the observed declines in sago abundance.

Invertebrates

Submersed macrophytes stabilize bottoms and in many instances provide much of the organic matter for zoobenthic food chains. Sago provides food and protection, as well as foraging and attachment sites, for many invertebrates (Moore 1915; Terrell 1923; Harrison 1962; Putshog 1973).

Accounts of sago's value to invertebrates vary. Some have suggested that sago beds are poorly to moderately attractive to invertebrates (Krecker 1939; Andrews and Hasler 1943), especially in moving-water environments (Needham 1938, cited in Moyle 1961; Greze 1953, cited in Hynes 1970) or openwater areas free of emergent plants (Berg 1949; Andrikovics 1973). Others have remarked about extremely large invertebrate populations supported by sago beds (Boltt 1973, cited in Howard-Williams and Davies 1979; Howard-Williams and Liptrot 1980). Zooplankton biomass in sago stands can reach 0.5 g C/m_2, with seasonal net annual production 3.5–6.0 g C/m_2 (Buchlovska 1964, cited in Korinek et al. 1987).

Studies by Moyle (1961), Krull (1970), and Andrikovics (1973) indicated that fine or feathery-leaved forms of submersed macrophytes supported more abundant invertebrate populations than broad-leaved forms, but a study by Korinkova (1971) seemed to disprove the idea that invertebrate den-

sites were related to degree of leaf dissection. Moreover, Krecker (1939) observed lower invertebrate density and diversity on sago than on several broader-leaved *Potamogeton*s.

Whatever the case, sago leaves are undissected but narrow and numerous, and, often in combination with algae, sago beds are heavily used feeding sites for waterfowl broods (Hochbaum 1944; Monda and Ratti 1988). These beds are prime sources of protein for young birds because of abundant and easily obtainable populations of macroinvertebrates, including diptera, trichoptera, odonata, chironomidae, and crustacea (G. A. Swanson and H. A. Kantrud, personal observation). Sago communities also provide escape cover for macroinvertebrates, thus allowing them to thrive in the presence of small fish. Jarvis et al. (1985) studied sago in a Nevada lake heavily used by largemouth bass (*Micropterus salmoides*), trout (*Salmo* spp.), and waterfowl broods and found that sago beds were attractive to ephemeroptera, tricoptera, chironomidae, and gastropoda during various seasons.

Filter-feeding and grazing forms predominate on sago (Howard-Williams and Davies 1979). In a large Saskatchewan lake where sago was the only submersed angiosperm, Huntsman (1922) found amphipod, copepod, and cladoceran crustaceans and notonectid, chironomid, and odonate insects abundant. The amphipod *Hyalella knickerbockeri* was most abundant in the sago beds, and the tricopteran *Phryganea interrupta* was restricted to them. Chironomid larvae were most numerous at stations occupied by sago in a shallow Iowa lake (Tebo 1955), and emerging adults were more abundant in sago than in either emergent communities or openwater areas of a shallow Manitoba marsh (Wrubleski 1987; Wrubleski and Roback 1987). Rich (1966) found *Tendipes*, *Oronectes*, *Anodonta*, and *Placobdella* in a Michigan wetland supporting sago. Abundant decapoda were associated with sago by Pirnie (1935).

In a Wisconsin reservoir, benthic macroinvertebrates numbered 25,000/m^2 in the upper 5 cm of sediment under sago beds, and some forms were recorded 10–15 cm deep (Miller et al. 1987). This density was only slightly less than in nearby beds of *Ceratophyllum demersum*, but >10 times that found at nearby unvegetated sites of approximately the same depth. Oligochaete worms were most common, followed by gastropods and chironomids.

Information on abundance of invertebrates in European, English, and African wetlands where sago was dominant or an important member of the submersed macrophyte community can be found in the studies of Hoffman (1958), Aleem and Samaan (1969a), Mason and Bryant (1975), Verhoeven (1980a), Howard-Williams and Allanson (1981), Davies (1982), Van Vierssen (1982a), Van Vierssen and Verhoeven (1983), Driscoll (1986), and Coetzer (1987). These sources indicate greatest occurrence in sago of crustacea, mollusca, diptera (mostly chironomid) larvae, and annelida. Other insect orders, especially coleoptera, hemiptera, heteroptera, and odonata, were often important.

The effects of underwater mowing on invertebrates associated with monospecific stands of sago were investigated by Stewart and Davies (1986) in an African estuary. The wetland was rather unusual because a tube-dwelling polychaete contributed most to the invertebrate biomass in the sago beds. With the exception of this organism, which colonized sago stems and leaf bases, mowing was deleterious to the other important forms, especially the long-lived, attached filter-feeders. The authors urged that some sago sites be left completely undisturbed in order that these organisms could fulfill their role as important food sources for birds and fish and possibly as reducers of algae-related water turbidity.

Direct burrowing, defoliating, feeding, and egg laying by invertebrates on living sago plants can be relatively unimportant, according to Berg (1949), who found that sago and several other narrow-leaved *Potamogeton*s were among the least used of 17 species of *Potamogeton* in Michigan lakes and rivers. However, laboratory studies show that Minnesota sago mass significantly decreases by snail (*Physa gyrina*) grazing (Sheldon 1987). Overall, the extent and effects of herbivory on submersed macrophytes is poorly understood.

Prejs (1986a,b, 1987) listed nematodes that penetrated the undergound parts of sago. The most common species, *Hirschmanniella gracilis*, causes necrotic yellow patches on rhizomes that can make up 10–50% of the rhizome mass. These nematodes may be most abundant on sago stressed by filamentous algae in polluted waters.

The chrysomelid beetle *Haemonia appendiculata* (Donaciinae) has recently become common in some marshes in the French Camargue, where damage to sago on the scale of hectares has been recorded (Grillas 1988). Artificial increases in water permanency and reductions in salinity presumably lead to the increase in dominance by sago and allow the development of high populations of this burrowing insect.

In summary, sago beds can be an important source of organic matter for zoobenthic food chains and provide many of the needs of a wide variety of invertebrates. Crustaceans, insects, and molluscs seem to be the most common macroinvertebrates associated with sago. These are also important foods of young waterfowl. Direct consumption of sago by invertebrates is relatively unimportant, but recent research reveals that a few species can significantly decrease sago biomass.

Amphibians and Reptiles

Turtles of the genera *Chelydra* and *Chrysemys* have been observed in Michigan in aquatic plant communities containing sago (McDonald 1951). Hoffman (1958) associated *Rana* and *Pelobates* frogs with brackish waters supporting sago in France. In an African wetland, Harrison (1962) found that *Rana-* and *Xenopus-*type tadpoles were common in sago. I often saw *Thamnophis-*type snakes swimming in sago beds up to 10 m from shore in Stump Lake in North Dakota.

Fish

Sago beds are important feeding, egg-laying, or rearing grounds for fish (Schiemer and Prosser 1976; McCarraher 1972, 1977; Howard-Williams and Liptrot 1980). Some of the largest stands of sago in the world occur in lakes that support commercial fisheries (Huntsman 1922; Aleem and Samaan 1969a; Skinner and Smart 1984). Changes in species composition of fish concurrent with a decline in sago biomass were recorded by Whitfield (1986). Individual wetlands are often managed to support both sago and fish because of their mutual importance to various types of avian wildlife. Moreover, in some instances, sago is harvested from lakes in order to encourage nutrient concentrations more conducive to fish production (Purohit et al. 1986). Fish also live in agricultural drainage ditches where sago is common (Driscoll 1986).

Sheldon (1987) found that excluding fish from aquatic plant communities in a Minnesota lake produced high snail densities and dominance by *Ceratophyllum demersum*, a common potential sago competitor. However, it is possible the plant increased because of lower light conditions in the exclosures. Gamefish are compatible with sago, but rooting species such as carp (*Cyprinus carpio*) will seriously lower sago production. Much information is available on carp–sago interactions, not only because this fish is a notorious destroyer of plants valuable to waterfowl and gamefish, but also because carp are often raised commercially in shallow wetlands where beds of sago and other submersed macrophytes form critical habitat for the invertebrate foods of carp. In addition, sago itself is a carp food.

In order to maintain sago and invertebrate production, carp must not be more than 1 year old when stocked and must be harvested at least every 2 years (Putshog 1973). They must not be stocked too heavily (Robel 1961a). Adult carp stocked at 530 kg/ha almost completely destroyed a well-established community of narrow-leaved *Potamogetons* and other submersed macrophytes in 51 days, but carp removed early in spring before intensive feeding began allowed rapid reestablishment of vegetation (Black 1946). In sago-dominated French wetlands, Crivelli (1983) found that 675 kg/ha carp destroyed half the dry weight of vegetation in 71 days. A prolific sago stand in an Australian lake was reduced to a few small patches after carp were introduced (Fletcher et al. 1985).

Adult carp feed and spawn in shallow (20–50 cm) water, where vegetation is prone to heavy damage (Crivelli 1983). Struthers (1930) found worst sago damage in shallow (<1.5 m) New York lake waters during the mid-May to mid-July carp breeding season; after breeding, the fish moved to luxuriant sago beds in 2.1–4.6 m of water where they caused little damage. Carp eggs can be abundant in sago beds (Harrison 1962) and deposited on the plants (Verhoeven 1980a). Struthers (1930) noted that the shallow-water stands of sago on which egg deposition occurred also provided young carp important escape cover from their fish predators. In some cases, carp can be restricted to deeper areas and have little effect on sago production (Sterling 1970).

Uprooting, not consumption, likely is the main direct effect of carp on sago; such uprooting is most critical when plants are immature (King and Hunt 1967). One-year-old carp are planktivorous (Matlak and Matlak 1976) and so should have little adverse effect on sago.

Carp feeding is evidenced by a dimpled appearance on bottom substrates where mouthfuls of sediment have been extracted and by bare trails among any remaining vegetation (Black 1946). King (1965) found depressions, up to 1.2 m wide and 15 cm deep, caused by carp activity in Michigan waters that sup-

ported sago, and Rich (1966), working in the same wetland, found such depressions could occupy up to 50% of the bottom area.

Common carp eat sago, but, unlike the herbivorous grass carp (*Ctenopharyngodon idella*) or its hybrids (see Control Methods) do not seem to consume large amounts except when stressed. Sago leaves composed 2.2% of the stomach content volume and were present in three of nine carp taken in Michigan sago beds (King 1965). In shallow mixosaline waters where invertebrate foods were plentiful, Sigler (1958) found that plants, including sago, composed 1–13% by volume of the diet of adult carp and up to 23% where normal foods were scarce. Nearly all the plant food was debris, although one fish contained 50 sago drupelets. Sigler (1958) also showed that young carp consume only small amounts of plant material, but that such material could be far more important in the diet of adult carp in cold infertile waters where invertebrate foods were scarce. Crivelli (1981, 1983) found no green vegetation in carp, but did find plant detritus and up to 1,000 seeds or drupelets of sago, *Scirpus maritimus*, and *Ranunculus baudotii*. These propagules were found in 88–93% of carp stomachs. Sago may be preferred as food by adult carp over *Ceratophyllum demersum*, *P. richardsonii*, and *Elodea canadensis*, in that order (Black 1946).

Sago is likely less affected by carp than several other submersed macrophytes because of the plant's prolific system of underground rhizomes and turions (Moyle and Kuehn 1964; King and Hunt 1967; MacCrimmon 1968). Nevertheless, carp exclusion or removal usually produces increased frequency or production of sago, probably because of improvements in water clarity (Anderson 1950; Tryon 1954; Jessen and Kuehn 1960; Moyle 1961; Robel 1961a; Baldwin 1968). Beule (1979) found that there was an inverse relation between carp populations and rake sample densities of submersed macrophytes, including sago.

Carp exclosures sometimes result in such greatly improved growing conditions for submersed macrophytes that sago abundance is reduced, probably by competition from other less turbidity-tolerant species (Threinen and Helm 1954). In at least some cases, sago can regain abundance 1 year after carp removal (Titcomb 1923) or reduction with toxicants (Garlick 1956). Carp population reduction with rotenone at Malheur Lake, Oregon, increased the sago-dominated area

by more than 6,000 ha the following year (Duebbert 1969).

According to Crivelli (1983)—who could not detect carp-caused turbidity in his study ponds but cited studies showing opposite results—high turbidity in carp ponds can depend mostly on bottom substrate and meterological conditions. In a turbid (Secchi depth 25–33 cm) Michigan wetland with carp present, sago occurred only at depths <51 cm but was found at depths up to 3.66 m after carp were removed (Lutz 1960). Rich (1966) cited unpublished data gathered by G. S. Hunt in a sago-inhabited Michigan wetland that showed Secchi depths increased from 33 cm to 117 cm in only 5 days after carp were poisoned, and that winds 32–40 km/h did not produce turbidity after such poisoning. King (1965) stated that, in a Michigan wetland that supported sago, carp-caused turbidity was not important at depths <45 cm and where Secchi depths were >30 cm. When carp occur in eutrophic wetlands subject to phytoplankton blooms, sago can be restricted to extremely shallow (<8 cm) sites (Kantrud 1984, unpublished). The activities of carp superimposed on that of domestic livestock nearly eliminated sago in one shallow wetland (Barnett 1964).

I conclude that sago beds are important to many species of fish. Young sago plants, especially in soft substrates in shallow water, can be harmed by the activities of bottom feeders like the common carp. Old plants can also be damaged, although reproduction from underground turions makes sago more resistant to carp damage than many other submersed angiosperms. Carp damage is greatest where fish are large and numerous. Only a few species of fish normally eat large amounts of sago.

Bird

Sago is world-renowned as a food of waterfowl and other aquatic birds (see Beneficial Values).

Several studies attempt to document the effects feeding waterfowl have on stands of sago. Waterfowl can excavate holes up to 10 m wide and 0.3 m deep in search of sago turions (Wetmore 1921). Sincock (1962) estimated that 9% of the fall sago crop was consumed by waterfowl, but his estimate did not include forage wasted during the feeding process. Sterling (1970) believed that a 52% removal of fall turions would not significantly decrease second-season productivity. Anderson and Low (1976) reported that waterfowl feeding activities reduced

peak standing crop and turions 40% and 43%, respectively, and postulated that a single stand could take heavy use over several seasons before production decreased. However, there was some evidence that heavy feeding on turions could reduce second-season standing crops. They also noted that reduction of that degree would be unlikely, because feeding waterfowl tended to move to more productive sites. Jupp and Spence (1977b) attributed 21% of the biomass removal in unenclosed stands of sago to waterfowl grazing. In their study area, underground turions were held tightly by clay bottoms, and waterfowl mostly clipped aboveground portions of the plants. Beds of sago were believed to have flourished for at least 20 years in a wetland that received very heavy use by sago-consuming waterfowl (Kantrud 1986a).

I found no references to significant decreases in sago production caused by activities of other groups of aquatic birds. Thus, given the extremely high reproductive potential of sago and its ability to shield at least some of its propagules from feeding birds, it is unlikely that birds are often a significant factor limiting sago production.

Mammal

Muskrats (*Ondatra zibethicus*) eat or otherwise use sago (McAtee 1911; Bednarik 1956; Gaevskaya 1966). I have seen the overwater portion of muskrat houses composed of at least 50% sago in some mixosaline North Dakota lakes where sago was the only submersed plant. *Potamogeton*s are listed as food for beaver (*Castor canadensis*) and moose (*Alces alces*), but sago is not specifically mentioned by Fassett (1940). Studies by Linn et al. (1972, 1975) showed that sago may be adequate forage for sheep and cattle if economic (presumably harvest and storage cost) and palatability problems can be overcome. Yeo (1965) stated that the starchy turions of sago can provide food for humans.

Economics

Beneficial

Waterfowl and Aquatic Bird Food

Jepson (1905) was perhaps the first to write in detail about the importance of sago as food for waterfowl. Many studies or observations since confirm the use of sago by both sexes of juvenile and adult waterfowl of many species in various parts of

the world. McAtee (1917) termed sago "the best all-round duck food in North America," and Martin et al. (1951) ranked the plant's food value to waterfowl as "the outstanding species in this outstanding genus."

All parts of sago are eaten by waterfowl (Appendix D). Pochards or diving ducks (Aythyini) and swans (Cygnini), and some species of geese (Anserini), are able to exploit foods in bottom sediments, and probably feed mostly on turions, whereas dabbling ducks (Anatini) and whistling or tree ducks (Dendrocygnini) likely consume mostly drupelets. Rhizome fragments or nearly whole plants often appear on the surface after being discarded by waterfowl that feed on turions. Much of this material is readily eaten by dabbling ducks and coots (*Fulica* spp.).

Sago consumption benefits waterfowl in other ways. Sago drupelets serve as a grinding media in waterfowl gizzards (Wetmore 1921), and the addition of green sago plants to the diet of penned mallards can reduce the toxic effects of lead pellets (Jordan and Bellrose 1951).

Evermann (1902), Jones (1940), Willi (1970), Borowiec (1975), Hurther (1979), Verhoeven (1980b), and several authors listed in Appendix D noted that coots have used sago extensively. Huge (90 km²) Lake Ichkeul in Tunisia has contained up to 20 km² of sago beds that have wintered up to 200,000 birds, including 70,000 coots (Skinner and Smart 1984). Dense sago beds can support coot nests (Harrison 1962). Sperry (1940) found that sago was consumed by the long-billed dowitcher (*Limnodromus scolopaceus*).

It has been recommended that the public be made aware of the importance of sago to wildlife in cases where the plant is otherwise considered a nuisance (Weisser and Howard-Williams 1982).

Water Quality

Lush stands of sago can take up sufficient P from water to suppress phytoplankton blooms, usually considered objectionable (Vermaak et al. 1981). Oxygen release by sago benefits filter-feeding organisms that may be important maintainers of water quality, especially in wetlands where sediments are largely anaerobic (Stewart and Davies 1986).

The importance of pollution-tolerant plants, such as sago, as biofilters of domestic sewage was extensively reviewed by Pieczynska and Ozimek (1976). They concluded that such plants are of no special significance, except in slightly polluted environ-

ments where plants must be regularly harvested before decomposition in order to reduce excess nutrients in the water. Harvest of sago along with other macrophytes has also proven ineffective or even detrimental in attempts to control phytoplankton through nutrient reductions in the water column (Neel et al. 1973).

Whitton et al. (1981) recommended that sago (as the only angiosperm) and four and five species each of algae and bryophytes be used for monitoring heavy metal pollution in rivers.

Property Protection

Putschog (1973) credited protection of shores and dams to the wave-dampening action of sago.

Detrimental

Sago is considered a noxious weed in waters used for recreational purposes such as swimming and pleasure boating (Harrison 1962; Hiltibran 1964; Vermaak et al. 1981). Besides physically obstructing such activities, sago can also serve as a substrate for nuisance algae at such sites (unpublished material, cited by Stewart and Davies 1986). Dunst and Nichols (1979) listed sago as one of the eight most common nuisance plants in Wisconsin lakes. The plant is considered a nuisance at religious bathing areas in India (Dutta and Gupta 1976) and provides suitable habitat for the intermediate host of the bilharzia disease parasite in Egyptian irrigation canals (Khattab and El-Charably 1986).

Sago is a notorious reducer of flows in irrigation ditches and waterways (Frank et al. 1963; Yeo 1965; Newroth 1974; Devlin et al. 1972; Mehta and Sharma 1976; Robson 1976; Moreria and Ferreira 1986). Sago can also aggravate flooding and cause unacceptably low nighttime O_2 minima in streams used to transport sewage effluent (Madsen et al. 1988). Dense carpets of sago and other submersed macrophytes are also said to limit movements of predator fishes, trap fish fry, and inhibit fishing (Titcomb 1923; Engel 1984). Masses of floating sago can also clog water intake bays at power plants (Peltier and Welch 1969).

Propagation and Management

Plant physiologists often select sago for experimental purposes because the plant can be grown in pure liquid media, which eliminates variables introduced by soils or other substrates. Sago is easily cultured from drupelets, turions, rhizomes, leafy tops, or cuttings in vessels either indoors or outdoors (Sauvageau 1894, cited in Muenscher 1936a; Moore 1915; Bourn 1932; Otto and Enger 1960; Teeter 1963; Yeo 1965; Huebert and Gorham 1983; Van Wijk et al. 1988). Vessels made of stoneware, wood, plastic, fiberglass, or glass are suitable. Either natural or artificially compounded liquid media and bottom substrates have given good results, as have tap water and garden soil. Water depth, illumination, circulation, and other environmental factors are varied according to the purposes of the experiment, but for best growth, temperatures are usually maintained at 20–22°C.

Moore (1915) and Muenscher (1936a,b) discussed storage and germination of sago drupelets and reviewed the early work of Sauvageau (1894), Crocker (1907), and Fischer (1907) on germination techniques. Drupelets can be stored either wet or dry, but wet storage in natural waters at temperatures just above freezing approximates the dormancy period for materials from temperate regions. McAtee (1911) urged that drupelets be planted immediately after harvest or removal from cold storage. Van Wijk (1983) observed best (40%) germination to occur when drupelets were dried for 3 months in sediment, ripened 14 months in room-temperature tap water, and placed in fresh water.

Turions can also be stored in water at low temperatures or packed in layers of saturated moss. Dry storage in straw at low temperatures is also recommended if turions are free of bottom soil. Turions can also be dipped in paraffin and stored for up to 4 years (Yeo 1965). Van Wijk (1983) found uniformly high (100%) germination indoors of turions produced in outdoor culture if the turions were allowed to remain in sediments through winter (stratification) and then were subjected to temperatures between 15°C and 25°C.

Many attempts have been made to establish large sago stands for wildlife (McAtee 1917, 1939; Terrell 1923; Bourn 1932; Martin and Uhler 1939; Sharp 1939; Steenis 1939; Donnelly 1968). Drupelets can be directly harvested or sometimes readily collected along lake shorelines after late summer storms. Even drupelets exposed on dry shorelines for more than 1 year in northern climates have given good germination in as little as 4–10 days. Drupelets can be broadcast in shallow water, but best results have been obtained with spring plantings of drupelets, turions, or plant tops imbedded in clay and dropped from boats. Recommended water depths are usually

<2 m. Turions or rhizomes can also be successfully planted in depressions cut with a metal pipe and then covered with a few centimeters of the parent substrate. Berge (1987) achieved best stands by planting single turions attached to nails with rubber bands or several turions in polyethylene produce bags weighted down with gravel; poorer stands resulted from plantings of turions contained in peat pots or with the older method where turions were imbedded in clay. All plantings were done inside snowfence enclosures (58 m^2) in naturally protected, open water areas.

Planting density of 3,000 plant parts per hectare is recommended. Delicate growth occurs the first season if sago drupelets are sown, but thick stands normally develop by the second season when root systems have become established.

It is not reasonable to expect great amounts of sago production from plantings made among potential competitors such as *Myriophyllum, Ceratophyllum, Ruppia,* and *Chara,* or in turbid or acidic waters or lakes of large fetch where wave action is severe. Best success can be expected in Cl- or SO$_4$-dominated waters with salinities 5–15 g/L. Davison and Neely (1959) stated that sago required waters with >50 mg/L alkalinity for successful propagation.

Waterfowl managers often attempt to increase sago through water level manipulations, but the results have been unpredictable. In a Michigan wetland, sago, in one season, replaced stands of *Polygonum lapathifolium* and *Echinochloa* spp. that had occupied dewatered areas the previous year; the sago germinated and grew in water <25 cm deep (Lutz 1960). Partial dewaterings in a Minnesota wetland resulted in a marked increase in sago growth and drupelet production and a decrease in less-desirable submersed macrophytes (Harris and Marshall 1963). Sago populations recovered well in an Iowa wetland dewatered for an entire growing season (Van der Valk and Davis 1978). In a eutrophic Ohio impoundment, sago did not increase greatly, but populations shifted to shallower waters after a partial winter drawdown, likely because of severe competition by the earlier-sprouting *Najas,* especially at deeper sites (Gorman 1979).

Long-term experiments in Utah to create openings in *Typha* stands to increase use by waterfowl have employed various combinations of dewatering, mowing, crushing, burning, applying herbicides, and blasting with explosives (Nelson and Dietz 1966).

Sago and other desirable waterfowl food plants replaced *Typha* on some plots, but others were invaded by the less desirable *Tamarisk.*

Waterfowl managers have had little success in restoring sago to former levels of abundance in waters populated with rough fish and high in calcium carbonate. In a Michigan wetland with a marl bottom, wind-caused turbidity early in the season lessened as sago growth developed, but was replaced by carp-caused turbidity during the middle of the growing season (Rich 1966). Ongoing experiments of Butler and Hanson (1985, 1986, 1988, unpublished) in a Minnesota wetland indicate that direct precipitation of calcium carbonate can add to wind- and fish-generated resuspension of calcium carbonate, silt, clay, and organic material and result in eliminating submersed macrophytes.

Sago increased dramatically in a Wisconsin wetland after two consecutive summer dewaterings that greatly reduced carp densities and likely released nutrients from highly organic bottom sediments (Linde 1965). Partial dewatering, followed by chemical treatments, contract fishing, the installation of an electric fish barrier to prevent spring spawning of carp, and the construction of breakwaters to create sheltered areas were done before a successful sago planting in a Wisconsin wetland (Berge 1987). Increases in sago also were sometimes noted when slightly brackish (2 g/L) wetlands in the prairie or aspen parkland region of Canada were subjected to partial or total dewaterings (Brent Wark, Ducks Unlimited Canada, personal communication). Many of these wetlands had not been dewatered for 20 years. The dewaterings were done to create interspersions of emergent plants and open water attractive to breeding waterfowl, rather than to increase submersed macrophytes. Nevertheless, partial drawdowns (e.g., water levels in a 1.2-m-deep wetland reduced to 0.3 m by August) usually resulted in an increase in all pondweeds, including sago. Results were more variable with complete drawdowns, where wetlands were kept dry most of the spring and summer and supplied with shallow water in early August, but in some instances, sago abundance was greatly increased over pre-drawdown conditions.

Natural recolonization of sago and other submersed macrophytes in areas where they have been absent for decades can occur with improvements in water quality, even in areas where it is unlikely that propagules are present. For instance, in the tidal Potomac River, it was suspected that sago propa-

gules were washed into the river from tributaries during spring runoff (Carter and Rybicki 1986).

Site preparation, harvesting techniques for propagules, propagule treatment and storage, and water management techniques for sago and other hydrophytes have been reviewed by Kadlec and Wentz (1974).

Control Methods

Chemical

This section reviews information on attempts to kill sago or control its growth with herbicides. Some of the chemicals mentioned may be considered unsafe for application to aquatic environments, and no endorsement of the use of any particular chemical is implied or intended. Readers are hereby advised to strictly adhere to application instructions on pesticide labels formulated by the U.S. Environmental Protection Agency.

Early efforts to control sago in irrigation ditches through use of aromatic solvents eliminated top growth and reduced turion numbers and size but did not eliminate turions completely (Otto et al. 1964; Ogg et al. 1969). Commercial granular fertilizers have been recommended for their ability to encourage phytoplankton and thus decrease water transparency so as to prevent pondweed invasion (Walker 1959a). Control of established stands with 2,4-D granules, silvex, or sodium arsenite has also been advised (Davison et al. 1962).

$CuSO_4$ algicide has been recommended at 0.05–0.11 ppm to control sago in still and flowing waters, but these rates are 10–20 times that needed to kill algae, and alkalinity of treated waters must be less than 150 ppm (Gangstad 1986). $CuSO_4$ browns sago leaves, shortens internodes, causes a bushy appearance, necrosis, and slows growth, but plants can survive 100 mg/L Cu concentrations for at least 21 days (Ryan and Riemer 1975).

Yeo (1967) considered the threshold of sago toxicity in reservoirs 125 ppb for diquat and 250 ppb for paraquat. Diquat at 26.7 ppm in flowing water controlled sago during the study of Hesser et al. (1972). Brooker and Edwards (1973) reported that sago replaced *Myriophyllum spicatum* in deeper waters after being treated with paraquat.

Frank et al. (1961) tested the effects of exposure time of eight herbicides on sago; for short-term exposure (30 min), diquat at 100 ppm gave the best control. Frank et al. (1963) later tested 91 herbicides and experimental compounds on sago in the laboratory and found that only 2 (fenac and dichlobenil), at 2.24 g/m^2, gave good control over four successive plantings. Fenac is easily absorbed by both above- and belowground parts of sago (Frank and Hodgson 1964).

When compared with controls (Devlin and Yaklich 1971), uptake of the herbicide naptalum was greater in young (30 days old) sago plants that were deficient in N or P. Thus control can sometimes be achieved with less than normal amounts of herbicide in nutrient-poor waters.

Devlin and Karczmarczyk (1975) found that norflurazon reduced chlorophyll content of sago, but growth was sustained by turions for 17 days. Sago is very sensitive to low levels of fluridone (Marquis et al. 1981). Sprouting plants can be controlled if sufficient light and contact time of 1–6 days can be attained (Anderson 1981). The Illinois Department of Conservation (1981) lists aquathol-K, aquizine, fenac, and ortho diquat in various forms and concentrations for sago control. Illinois sago was routinely treated with all these chemicals except fenac by 1984 (Tazik and Wiley 1984). Heavy sago infestations in Arizona municipal and industrial water canals have been controlled sucessfully with repeated applications of an endothall derivative at 0.2 ppm (Corbus 1982). Acrolein has given good control of sago and has been used for more than 10 years in Egyptian irrigation canals (Khattab and El-Charably 1986). Lawrence (1962) and Newroth (1974) listed herbicides used to control sago and other plants.

Sago was controlled with 2,4-D butoxethanol ester pellets (29% active ingredient) applied at a rate of 168 kg/ha (Dutta and Gupta 1976). Getsinger et al. (1982) used a helicopter to drop 112 kg/ha of 20% acid equivalent granular 2,4-D on a community of introduced *Myriophyllum spicatum*, sago, and other native submersed macrophytes. Once the *M. spicatum* disappeared, greater wave action stirred bottom sediments and increased turbidity, reducing Secchi disk transparency from >1.5 m to <0.3 m. Native submersed macrophytes began to disappear during the third post-treatment week, and 1 week later a phytoplankton bloom (which also contributed to turbidity) was observed. Sago was still absent from the area 4 years later, at which time *M. spicatum* had attained 10% of its former biomass. Westerdahl and

Hall (1983) listed the threshold concentration of 2,4-D needed to control sago as 0.1–0.25 mg/L.

Correll and Wu (1982) found that photosynthesis of sago was inhibited by dissolved atrazine at 650 μg/L but stimulated by 75 μg/L. Hartman and Martin (1985) tested three common herbicides (glycophosphate, atrazine, and alachlor) and one insecticide (carbofuran) for their inhibiting effects on the growth and sprouting of sago turions. None of the chemicals affected sprouting; atrazine inhibited growth at all concentrations, glycophosphate stimulated growth at intermediate application levels, carbofuran had no effect, and alachlor was stimulatory at low levels and inhibitive at high levels. Sago was affected by a triazine herbicide at 125 ppb (Fowler 1977).

Physical and Biological

I found no references for any cost effective means to physically control sago growth on large areas. Results of such efforts are often temporary (Mitzner 1978). Use of large rakes, cables, and mechanical harvesters to remove sago is notoriously expensive and labor intensive (Gangstad 1986). Sago beds have been killed on small areas by a cover of black plastic sheeting for 10–18 days (Mayhew and Runkel 1962). Similarly, biomass of sago and other submersed plants has been reduced >80% in small recreational areas by anchoring fiberglass screens to the bottom with bricks (Engel 1984). Physical blanketing is impractical unless goals justify the labor and maintenance involved. Commercial blue and brown dyes introduced to the water column can suppress light and eliminate *Potamogetons* in enclosures, but the technique was not tried on sago (Buglewicz and Hergenrader 1977).

Control of submersed macrophytes with mechanical harvesters can sometimes result in increased density of sago the following growing season (Neel et al. 1973), likely because of reduced competition. Mechanical harvesting of sago and other macrophytes can also cause the number of morphologically shorter plants to increase (Engel 1984). Successful control of sago by underwater mowing can require three cuts per year in areas with long growing seasons (Weisser and Howard-Williams 1982). Mechanical harvesting in streams is often inefficient because of stream morphology (Madsen 1986). Madsen et al. (1988) found that sago in a stream needed to be mowed every 2 weeks to maintain a basal biomass level of 18% of preharvest levels and every 8 weeks to maintain 44%; harvesting delayed flowering and senescence.

Growth of sago having root zone in the upper 3 cm of substrate can be suppressed for about 6 months in irrigation canals in India by drying canal bottoms in the sun for 5 days (Malhotra 1976).

Many types of plants and animals have been used or suggested for use to control submersed hydrophytes. For sago control, only fish have been extensively studied. I found two suggestions for using vascular plants to control sago. Yeo (1976) indicated that plantings of the short emergent macrophytes *Eleocharis acicularis* and *E. coloradoensis* could prevent sago from establishing in shallow waters. Madsen (1986) indicated the possibility of controlling sago in streams by growing shade trees along the banks to reduce light.

The burrowing chrysomelid beetle *Haemonia appendiculata* (Donaciinae) has been shown to cause great, although temporary, damage to sago in fresh to oligosaline wetlands having permanently flooded water regimes and has been suggested as a promising biological control agent for the plant (Grillas 1988).

The grass carp (*Ctenopharyngodon idella*) was introduced to United States waters for aquatic plant control in 1963 and much controversy over the ecological consequences of this act has resulted (Leslie et al. 1983). Studies in Europe and Asia cited by Cross (1969), Opuszynski (1973), and Fowler and Robson (1978), and work in the United States (Duthu and Kilgen 1975; Swanson 1986a; Wiley et al. 1986; Bowers et al. 1987) showed that sago is at least moderately, or more likely highly, preferred as food by the grass carp or hybirds of the grass carp and common carp or bighead carp (*Hypophthalmichthys nobilis*). Mehta et al. (1976) found that Indian sago became a highly preferred food of grass carp when the fish attained a weight of 200 g.

Grass carp ($\bar{x}$ wt, 217 g) stocked at 116–688 kg/ha shifted from a diet of sago to that of nonpreferred species, but the sago recovered 1 year following fish removal (Fowler and Robson 1978). The feeding activities of grass carp reduced the July dry weight biomass of mixed stands of sago and *P. nodosus* from 1,400 g/m^2 to 24 g/m^2 in 4 years, but after about 3 years the grass carp biomass began to decline, and by the fourth year carp biomass decreased to levels attained during the second year after stocking (Mitzner 1978). These fish ate large amounts of *Potamo-*

geton. Subsequent stockings of grass carp in many farm ponds in the central United States showed that this fish eliminated almost all submersed macrophytes and that the desired partial control of these plants is very difficult (L. Mitzner, personal communication). It is likely that grass carp singled out and consumed all the aboveground parts of a highly productive (aboveground biomass 829.6 g/m^2) sago–*Chara* community in a Russian floodplain lake where the fish were common.

Latest research has focused on use of sterile diploid and triploid grass carp for control of sago and other submersed plants, because grass carp overpopulation has had adverse effects on gamefish habitat (Bowers et al. 1987). These fish retain more than 90% of the phosphorus consumed when artificially fed sago and may be an effective means to remove phosphorus from aquatic systems (Chapman et al. 1987). Modeling efforts by Wiley et al. (1984) indicated that triploid grass carp were far more cost effective than chemicals for either suppressing or eradicating a community dominated by sago and naiads (*Najas* spp.). In some areas of Egypt, harvesting of grass carp used for sago control in irrigation waterways resulted in a net profit (Khattab and El-Charably 1986).

Schwartz et al. (1986) found that sago dry weight was reduced from 4.9 g/m^2 to 0.2 g/m^2 and 2.1 g/m^2 by the addition of (respectively) 500 and 2,500 blue tilapia (*Tilapia aurea*) per hectare in experimental ponds. However, sago was not the dominant plant in the ponds studied, and these authors postulated that control of vegetation in these ponds was through uprooting, deleafing, and increases in turbidity.

Submersed macrophytes are undesirable in artificial fishponds because they make fishing difficult and tie up nutrients. Fertilizers are often added to these ponds to stimulate phytoplankton, which then compete with and decrease vascular plants, but I could find no reference as to whether this technique is effective against sago.

Research Needs

Only a few of the hundreds of species of submersed macrophytes are important foods of waterfowl and other aquatic birds. A single sago-dominated lake can support a large percentage of the continental population of an important waterfowl species for a month during fall staging period (Kantrud 1986a),

and I suspect that the migration routes of some mostly herbivorous waterfowl are determined by traditional access to a relatively small variety of submersed plant foods. Yet, the effects of herbivory on standing stocks of these economically important plants and their potential competitors are just beginning to be revealed. For example, recent work by Sheldon (1987) shows that snails can consume up to 13% of the total leaf area of submersed plants in Minnesota lakes. The basic question of whether herbivory or detritivory form the basis for secondary production in littoral ecosystems is unanswered, because algal and macrophyte productivity and the factors influencing them are so poorly understood (Murkin 1989).

Further research seems warranted on the importance of genetic adaptation of sago to various basic environmental factors because modern society has created many threats to natural plant communities. Recent work by Van Wijk (1988, 1989) and Van Wijk et al. (1988) on genetic adaptations to salinity and the habitat factors that determine whether sago reproduces sexually or asexually likely could be, perhaps with reciprocal transplant experiments, expanded to include factors such as substrate type, nutrient availability, or water level fluctuation. Such information could help identify and protect sago genotypes suitable for future use to revegetate seriously altered or disturbed aquatic ecosystems.

Davies (1982) showed that the loss of sago in a brackish wetland drastically depleted the invertebrate community, and that the replacement primary producers did not provide enough shelter, food, or surface area for attachment to maintain large standing stocks of the primary and secondary consumers. Howard-Williams and Liptrot (1980) pointed out that such ecosystems may be especially vulnerable to catastrophic losses of primary production, because so few submersed macrophytes are able to tolerate brackish waters that show wide fluctuations in salinity. In heavily populated areas, commonly observed problems of eutrophication and siltation are often complicated by the effects of special industrial effluents, thermal pollution from electrical power plants, and hydrological changes resulting from dredging and filling operations. Other areas show increased use of sophisticated agricultural chemicals and pesticides. Controlled experiments that simulate the effects of human developments on a wide range of wetland types are needed to determine how to prevent productivity losses and maintain species diversity.

From a wildlife standpoint, corrective actions require that biologists understand the mechanisms responsible for the deterioration of sago and other high quality waterfowl food plants in waterfowl staging, migration, and wintering areas. These places usually are deeper wetlands that also support fish populations. Especially needed are experiments to identify the causes of light-limiting turbidity. Similarly, experiments must address the trophic interactions between benthic omnivorous fish, planktivorous fish, zooplankton, and phytoplankton and their effects on water chemistry and vascular plant communities, in wetlands managed primarily for waterfowl. An important unanswered question for waterfowl managers is whether fish removal, manipulation of existing populations, or altering the predator–prey relations of fish populations through stocking can economically and permanently increase the abundance of sago and other valuable waterfowl food plants (Spencer and King 1984). Such research is currently under way in a Minnesota lake where it is suspected that increased water levels and introductions of rough fish initiated a complex series of events leading to light-limiting calcite accumulations in the water column (Butler and Hanson 1985, 1986, 1988, unpublished).

There is a need to greatly improve our ability to predict the response of sago and other hydrophytes to vegetation management in the shallow prairie wetlands that are the breeding areas for most of North America's waterfowl (Kantrud 1986b). In most of these wetlands, water control structures are not present, and managers are limited to only a few tools (prescribed burning, grazing, mechanical treatments, and herbicide applications). The usual goal here is to maintain mixtures of stands of emergents—used for nest sites and escape cover—and beds of submergents—used for feeding areas. Prairie wetlands lie in basins of extremely diverse hydrological setting, so methods must be developed to manage hydrophytes across wide gradients of water chemistry and water permanency in a region where long-term cycles of drought and excess precipitation occur.

Much needs to be learned on how to establish and maintain sago and other submersed hydrophytes that are valuable waterfowl foods in manmade and natural wetlands where water control structures allow dewaterings or significant water level manipulations. Light-limiting turbidity, rough fish, excessive emergent vegetation, sedimentation, and untoward water level fluctuations are common features of many of these wetlands. Personnel are often asked to manage these areas simultaneously as flood control reservoirs, recreational boating areas, sport fisheries, and waterfowl hunting areas. It is especially important that managers know the dewatering schedules and rates of water level increase that would allow sago and other hydrophytes to germinate and grow. Gibbs (1973) suggested that much more information would be required to explain the little-understood cycles between dominance by phytoplankton, macroalgae (*Chara*), and *Potamogeton* in wetlands important to waterfowl and fish. Cooke (1980) called for research to determine proper dewatering intervals, effects of season of dewatering on such intervals, effects of dewatering on sediment and water column chemistry, and if the efficacy of the technique could be enhanced by combining it with other plant management methods. Finally, he emphasized the need to develop better evaluation techniques when vegetation manipulations are undertaken.

For sago control, Spencer (1986a,b) suggested pursuing research into management techniques that would disrupt turion formation sufficiently to result in the production of smaller turions. This could result in smaller plants more susceptible to environmental stress. Also recommended was the delaying of control techniques until after carbohydrate reserves in turions are exhausted.

Acknowledgments

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Appendix A. Sago Pondweed Biomasses[a] and Probable Factors Limiting Biomass

Reference	Total or aboveground biomass (g/m^2 dry wt)[b]	Code to limiting factors[c]															
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Ozimek et al. 1986	<5						x										
Kautsky 1987	<5		x									x					
Schiemer and Prosser 1976	12	x	x		x		x				x						
Kautsky 1987	<18													x			
Jerling and Linde 1977	25		x	x	x												
Singh 1981	25		x		x											x	
Sahai and Sinha 1976	<31						x										
Ozimek et al. 1986	<44			x													
Taylor 1983	52	x															
Filbin and Barko 1985	55	x	x														
Van Wijk 1988	55			x													
Van Wijk 1988	73	x	x	x				x									
Van Wijk 1988	78			x									x				
Lutz 1960	<79	x	x			x											
Boynton and Heck 1982	<100	x															
Bernatowicz 1969	100		x														
Jupp and Spence 1977b	104	x					x	x									
Rich 1966	107	x								x							
Oglesby et al. 1976	118	x	x	x	x												
Westlake 1961	123	x					x										
Congdon and McComb 1981	<132		x						x								
Van Wijk 1988	133			x		x											
Brooker and Edwards 1973	141					x											
Sterling 1970	165		x														
Vermaak et al. 1981	174	x					x										
Davis and Carey 1981	175	x															
Ravanko 1972	<190		x											x			
Kvet and Husak 1978	200	none indicated															
Gopal et al. 1978	214	none indicated															
Jensen 1940	<227	x							x								
Madsen 1986	227			x													
Van Wijk 1988	237			x										x			
Vanamburg (n.d.)	264	none indicated															
Huber 1952	>266	x			x												
Kaul et al. 1978	<272	none indicated															
Ozimek et al. 1986	275	none indicated															
Kollman and Wali 1976	<293								x							x	x	x
Van der Valk and Bliss 1971	<297	x			x						x						
Krausch 1976, cited in Wallentinus 1979	<300	none indicated															
Anderson and Low 1976	<316				x		x										
Craner 1964	<317						x	x	x								
Van Wijk 1988	327		x														

Appendix A. *Continued.*

Reference	Total or aboveground biomass (g/m² dry wt)[b]	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
		Code to limiting factors[c]															
Anderson and Jones 1976	<350			x	x	x											
Van Wijk 1988	376							x									
Sinha 1970	<370	none indicated															
Low and Bellrose 1944	<392	x				x											
Van Wijk 1988	392							x									
Sahai and Sinha 1976	<445	none indicated															
Van Wijk 1988	583					x											
Madsen et al. 1988	620	none indicated															
Van Wijk 1988	668					x											
Peterka and Hanson 1978	716	none indicated															
Kollman and Wali 1976	732	none indicated															
Barker and Fulton 1979	880	none indicated															
Gaevskaya 1966	900	none indicated															
Olson 1979	<954				x	x		x									
Madsen 1986	992	none indicated															
Van Wijk 1988	1,313	none indicated															
Shubert 1982	1,500	none indicated															
Aleem and Samaan 1969b	<1,568	x		x		x											
Howard-Williams 1978	1,952	none indicated															
Zaky 1960	1,988	none indicated															
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16

[a] Wet weight conversion to dry weight: multiply by 0.14; g C/m² conversion to dry weight: multiply by 1.54; ash-free dry weight conversion to dry weight: multiply by 1.34.

[b] Total biomass listed if above- and belowground biomass values given.

[c] Codes: 1 = Turbidity; 2 = Other macrophytes or epiphytes (potential competitors); 3 = Wave, wind, or current action (exposure or erosion of substrate); 4 = Insufficient or excessive depth; 5 = Water level fluctuations (mostly decreases); 6 = Pollution or eutrophication; 7 = Waterfowl grazing; 8 = Excessive salinity; 9 = Uprooting by fish; 10 = Siltation; 11 = Ice action; 12 = Rocky substrate; 13 = Growth form; 14 = Insufficient nutrients; 15 = Toxic elements; 16 = Excess energy demand.

Appendix B. Origins of Nutrient Enrichment in Wetlands Where Sago Pondweed Occurred

Reference	General (source undetermined)	Agricultural runoff (fertilizer and silt)	Feedlot runoff	Sewage effluent	Industrial effluent
Boye Petersen 1917, cited by Olsen 1950			x	x	
Pirnie 1935					x
Van Donselarr et al. 1961	x				
Westlake 1961				x	
Hunt 1963	x				
Spence 1964	x				
Volker and Smith 1965		x		x	
Kaul and Zutshi 1967				x	
Lind and Cottam 1969		x			
Peltier and Welch 1969					x
Kohler et al. 1971				x	
Stuckey 1971		x		x	
Perkins and Abbott 1972	x				
Neel et al. 1973				x	
Jupp et al. 1974	x				
Haslam et al. 1975	x				
Pieczynska et al. 1975				x	x
Wilson et al. 1975	x				
Andersen 1976				x	
Krausch 1976	x				
Pieczynska and Ozimek 1976				x	x
Sahai and Sinha 1976				x	
Schiemer and Prosser 1976				x	
Holmes and Whitton 1977				x	x
Wiegleb 1978				x	
Ho 1979		x		x	
Jupp and Spence 1977a		x	x		x
Fetter et al. 1978		x		x	x
Haslam 1978	x				
Hejny and Husak 1978	x				
Leah et al. 1978		x			
Peterka and Hanson 1978	x				
Pip 1978	x				
Ozimek 1978				x	
Carpenter 1979	x				
Dunst and Nichols 1979	x				
Lachavanne 1979	x				
Vass 1980				x	
Janauer 1981	x				
Merry et al. 1981	x				
Vermaak et al. 1981					x
Shubert 1982	x				
Vander Zouwen 1982		x		x	
Ozimek and Kowalczewski 1984				x	

Appendix B. *Continued.*

Reference	General (source undetermined)	Agricultural runoff (fertilizer and silt)	Feedlot runoff	Sewage effluent	Industrial effluent
Filbin and Barko 1985		x			
Madsen and Adams 1985		x		x	
Peverly 1985		x			
Blake et al. 1986				x	
Madsen 1986		x		x	
Stewart and Davies 1986		x		x	x
Penuelas and Sabater 1987		x			x
Madsen et al. 1988				x	

Appendix C. Bottom Substrate Types Supporting Sago Pondweed Growth

Reference	Sand	Silt	Clay	Loam	Organic
Wetmore 1921			x		
Bourn and Jenkins 1928					x
McAtee 1939	x				
Sharp 1939					x
Jensen 1940			x	x	
Wilson 1941	x	x			x
Low and Bellrose 1944			x		
Thomson 1944	x				x
Olsen 1945	x				
Sigler 1948	x				
Brumsted and Hewitt 1952			x		
Tryon 1954	x				
Tebo 1955					x
Jessen and Kuehn 1960		x			
Harrison 1962			x		
Craner 1964			x		
Spence 1964	x				
Sincock 1965				x	
Smeins 1965					x
Dix and Smeins 1967	x				
Sterling 1970		x			
Kohler et al. 1971					x
Lundegardh-Ericson 1972			x		x
Bergman 1973		x	x		
Anderson and Jones 1976	x	x		x	
Oglesby et al. 1976		x			
Gladyshev and Kogan 1977		x			
Robarts and Allanson 1977	x				
Haslam 1978		x			
Verhoeven and Van Vierssen 1978a	x				
Howard-Willams and Davies 1979	x				
Wallentinus 1979	x				
Purohit 1981			x		
Getsinger et al. 1982	x				
Van Vierssen 1982a					x
Thorne-Miller et al. 1983					x
Carter et al. 1985b		x			
Madsen and Adams 1985	x				
Madsen 1986	x	x			
McConville et al. 1986	x				
Wolseley 1986			x		
Hammer and Heseltine 1988	x				

Appendix D. Use of Sago Pondweed[a] as Food by Groups of Waterfowl

Reference	Waterfowl (general)	Diving ducks	Dabbling ducks	Geese	Swans
McAtee 1911		1			
McAtee 1917		2			
McAtee 1918			2		
McAtee 1922			3		
McAtee 1939	2				
Moore 1915		6			
Mabbott 1920			3		
Oberholzer and McAtee 1920	3,6				
Wetmore 1921	2				
Phillips 1923	3				
Terrell 1923	1				
Metcalf 1931	3,6				
Kubichek 1933		3,4,5,6			
Pirnie 1935	3,6				
Christensen 1938	1				
Bennett 1938			1		
Cottam 1939		3,4,5,6			
Martin and Uhler 1939	3,4,5,6				
Jensen 1940	1				
Bellrose and Anderson 1943	1				
Moyle 1945	3,6				
Moyle and Hotchkiss 1945	3,6				
Campbell 1946			2	2	
Smith 1946		3,6			
Erickson 1948		3,6			
Stollberg 1950	3				
Yocom 1951		1			
Harris 1952		1	1		
Huber 1952		1	1		
Hancock 1953	3				
Kortright 1953		3,6	3,6	3,6	3,6
Nelson 1954	6			6	6
Cronan 1957		1			
Gates 1957			1		
Hoffman 1958		3,6			
Anderson 1959		3,4,6			
Davison and Neely 1959	1				
Sherwood 1959					1
Lutz 1960		1	1		
Perret 1962			1		
Quay and Critcher 1962		3,4,6	3,4,6	3,4,6	
Sincock 1962		1			
Stewart 1962		3,6			3,6
Craner 1964		3,4,5,6			3,4,5,6
Gaevskaya 1966	1			1	1
Cronan and Halla 1968		1	1		
Bartonek and Hickey 1969a,b		5,6			

Appendix D. *Continued.*

Reference	Waterfowl (general)	Diving ducks	Dabbling ducks	Geese	Swans
Duebbert 1969		1			1
Olney 1969		1			
Sterling 1970	6			6	6
Watson et al. 1970		3	3	3	
Hocutt and Dimmick 1971			5,6		
Kerwin and Webb 1972			1		
Bergman 1973		5,6			
Paullin 1973	3,6				3,6
Sugden 1973			3,6		
Anderson and Low 1976		2,3,6	2,3,6		2,3,6
Serie and Swanson 1976			4		
Jupp and Spence 1977b			3,4,6		3,4,6
Dirksen 1982					1
Munro and Perry 1982		1			
Thomas 1982		3			
Wishart 1983			3,4		
Bailey and Titman 1984		3,4,5,6			
Skinner and Smart 1984	1				
Noyes and Jarvis 1985		6			
Gerbeaux and Ward 1986					1
Jarvis and Noyes 1986		6			
Swanson 1986b		1	1		
Anderson and Ohmart 1988	1				
Korschgen et al. 1988		3,6			
Van Wijk 1988			1		1

[a]1 = unknown or no specific parts mentioned; 2 = whole plant; 3 = drupelets; 4 = leaves; 5 = rhizomes or stems; 6 = turions.
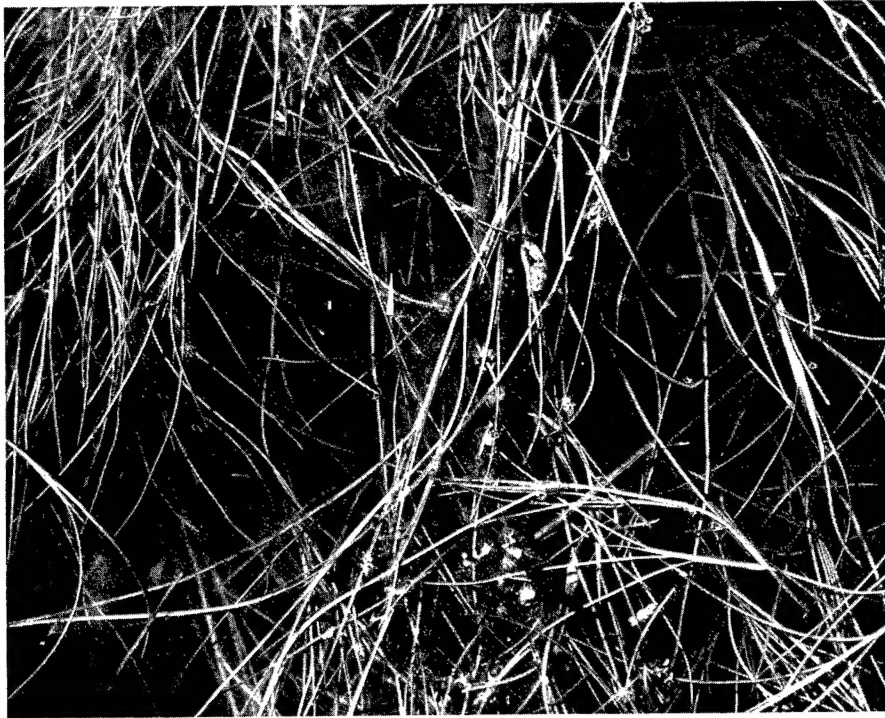
Sago pondweed serves as host to an abundance of small animals and plants, such as this attached filamentous algae, that inhabit an aquatic community.
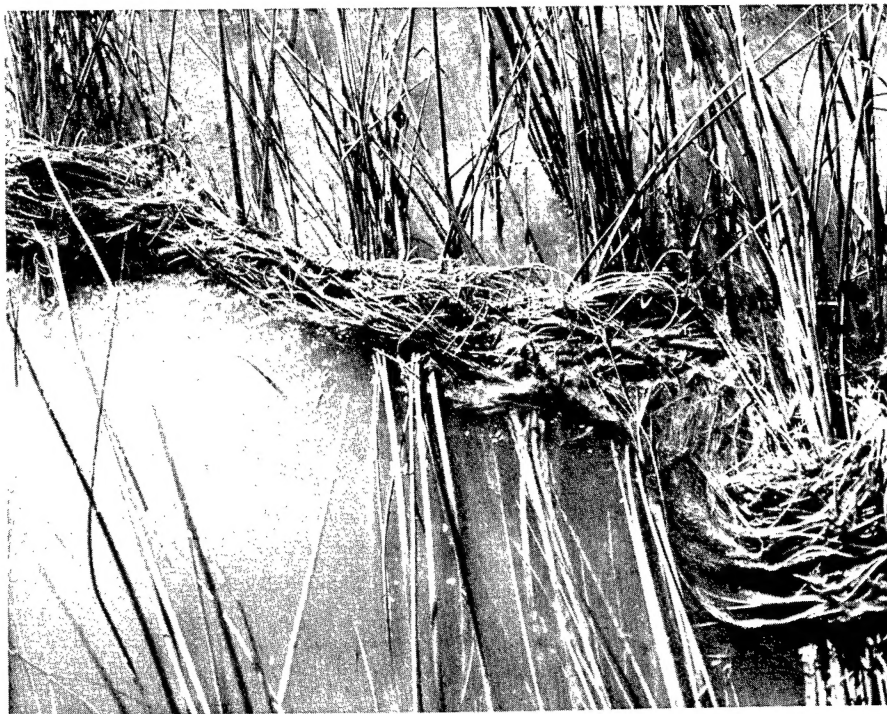
In migration, waterfowl feed on, and uproot, large amounts of sago pondweed which washes into emergent weeds and accumulates along shorelines. This occurs most often during fall in north temperate regions when sago becomes senescent.

Kantrud, Harold A. 1990. **Sago Pondweed (*Potamogeton pectinatus* L.): A Literature Review.** U.S. Fish Wildl. Serv., *Resour. Publ.* 176. 89 pp.

Sago pondweed (*Potamogeton pectinatus* L.) is an internationally important aquatic food plant for waterfowl; the tubers especially being a carbohydrate-rich source of nutrition. Sago has adaptive growth forms and reproductive strategies that provide genetic ecotypes to survive many habitat and environmental stresses. Its tolerance to drought, strong salinity and alkalinity, nutrient-rich waters, polluted habitats, and a wide range of rooting substrates is singular among *Potamogeton* species. Sago's dominance in a community usually is correlated with environmental changes. Turbidity is the factor that most often limits sago growth. Although seeming to prefer stable water levels, the plant can tolerate considerable fluctuations. Sago pondweed's mat-forming habits are often a nuisance in irrigation canals and in recreational areas, requiring control. A large body of foreign and American literature on sago pondweed is reviewed and summarized, with recommendations presented for research on growth-limiting and on production-stimulating methods to benefit waterfowl.

Key words: Sago pondweed, *Potamogeton pectinatus*, autecology, physiology, habitat, economics, management, control.

A list of current *Resource Publications* follows.

166. Checklist of Vertebrates of the United States, the U.S. Territories, and Canada, by Richard C. Banks, Roy W. McDiarmid, and Alfred L. Gardner. 1987. 79 pp.
167. Field Guide to Wildlife Diseases. Vol. 1. General Field Procedures and Diseases of Migratory Birds, by Milton Friend, Cynthia J. Laitman, and Randy Stothard Kampen. 1987. 225 pp.
168. Mourning Dove Nesting: Seasonal Patterns and Effects of September Hunting, by Paul H. Geissler, David D. Dolton, Rebecca Field, Richard A. Coon, H. Franklin Percival, Don W. Hayne, Lawrence D. Soileau, Ronnie R. George, James H. Dunks, and S. Dwight Bunnell. 1987. 33 pp.
169. Saltcedar Control for Wildlife Habitat Improvement in the Southwestern United States, by Theodore A. Kerpez and Norman S. Smith. 1987. 16 pp.
170. Pesticide Use and Toxicology in Relation to Wildlife: Organophosphorus and Carbamate Compounds, by Gregory J. Smith. 1987. 171 pp.
171. Sand and Gravel Pits as Fish and Wildlife Habitat in the Southwest, by William J. Matter and R. William Mannan. 1988. 11 pp.
172. Satellite Telemetry: A New Tool for Wildlife Research and Management, by Steven G. Fancy, Larry F. Pank, David C. Douglas, Catherine H. Curby, Gerald W. Garner, Steven C. Amstrup, and Wayne L. Regelin. 1988. 54 pp.
173. Key to Acanthocephala Reported in Waterfowl, by Malcolm E. McDonald. 1988. 45 pp.
174. Obsolete English Names of North American Birds and Their Modern Equivalents, by Richard C. Banks. 1988. 37 pp.
175. Procedures for the Analysis of Band-recovery Data and User Instructions for Program MULT, by Michael J. Conroy, James E. Hines, and Byron K. Williams. 1989. 61 pp.

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